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The Role of Allelopathic Interference in the Maintenance of Southern Appalachian Heath Balds

Robert Edward Gant
University of Tennessee - Knoxville

To the Graduate Council:

I am submitting herewith a dissertation written by Robert Edward Gant entitled "The Role of Allelopathic Interference in the Maintenance of Southern Appalachian Heath Balds." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

E. E. C. Clebsch, Major Professor

We have read this dissertation and recommend its acceptance:

Clifford C. Amundsen, John P. Witherspoon, Frank W. Woods, James W. Hilty

Accepted for the Council:

Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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Edward S. C. Clebsch

E. E. C. Clebsch, Major Professor

We have read this dissertation
and recommend its acceptance:

Clifford C. Hassa

Frank W. Woods

James W. Hardy

John P. Witherspoon

Accepted for the Council:

L. Evans Roth

Vice Chancellor
Graduate Studies and Research

THE ROLE OF ALLELOPATHIC INTERFERENCE IN THE MAINTENANCE OF SOUTHERN APPALACHIAN HEATH BALDS

A Dissertation

Presented for the

Doctor of Philosophy

Degree

The University of Tennessee, Knoxville

Robert Edward Gant

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ABSTRACT

Allelopathic interference seems to be an important mechanism in the maintenance and persistence of southern Appalachian heath bald communities. Comparative analyses were conducted on two heath balds located in the Balsam Mountains of western North Carolina to distinguish phytotoxic characteristics that enhance persistence. Field studies revealed that one community was a mixed heath bald dominated by Rhododendron catawbiense and the second resembled an immature spruce-rhododendron forest heath dominated by Rhododendron maximum and Picea rubens.

Caffeic acid, gallic acid, gentisic acid, hydroquinone, p-hydroxybenzoic acid, 2-pinene, phloroglucinol, rhododendrol, and vanillic acid were isolated and identified from canopy drip, leaves, litter, roots, and soil of the two heath balds. Bioassays run with aqueous leachates of heath bald litter and soil produced varying degrees of radicle reduction in three test species. Long-term inhibition by heath bald soils was confirmed in greenhouse experiments. Field studies demonstrated that environmental forces increased the allelopathic effectiveness of heath bald soils on seedling growth and survival.

Influx of seed from the surrounding forests was sufficient to sustain invasion pressure against both heath balds.

Allelopathic interference delays successional replacement of Rhododendron maximum heath balds by partially suppressing the establishment and growth of forest competitors. Heath balds dominated by Rhododendron maximum cannot maintain themselves and represent truly successional communities.

Rhododendron catawbiense heath balds represent stable communities that employ allelopathic interference to arrest succession and maintain themselves. Communities of this type can be expected to persist in the southern Appalachian forests.

Investigations of southern Appalachian heath balds revealed that these communities are more diverse and more involved in the succession of the regional vegetation than has been previously recognized.

Key words: allelopathy, interference, heath balds, phytotoxins, inhibition, persistence, stability, resilience, Rhododendron, Kalmia, phenols, Appalachian, seed rain, litterfall, root biomass, succession.

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CHAPTER I

INTRODUCTION

The shrub heath communities of the southern Appalachian Mountains present a locally unique physiognomic and ecological contrast to the surrounding forests. The discontinuity that these shrubs impose upon the forest profile is so distinct that they are referred to locally as "slicks" or "balds." Cain (1930) formally proposed the term "heath bald" to describe all treeless areas of the region dominated by plants of the order Ericales (Ericaceae).

Heath balds occur over a broad range of elevations, topographic positions, and geologic substrates within the southern Appalachians. Their frequency in this region suggests an ability to sustain shrub dominance against forest encroachment through an interference mechanism.

Interference, as described by Muller (1969), embraces all forms of reaction by one plant that deleteriously affects another. The concepts of allelopathy and competition have been incorporated into this definition as mutually exclusive subsets of the mechanisms of interference. These mechanisms are distinguishable by additions or deletions to the environment. Allelopathy differs from competition by requiring the introduction of phytotoxins rather than the preemption of a vital resource.

Expression of interference by heath bald constituents is likely to be the result of complex interactions among allelopathic and physical environmental factors. Allelopathic interference is suggested by the broad ecological amplitude of heath balds and their similarity to other sclerophyllous shrub communities of demonstrated allelopathic interference (Muller et al. 1964).

This work tests the hypothesis that heath balds can persist as distinct entities through allelopathic interference. The investigation was designed to evaluate individual heath bald species, their interactions, and their accumulative effects in producing allelopathic interferences. Two distinctly different heath bald communities served as case studies for this investigation. Figure 1 presents the conceptual model used to define the major areas of investigation on both heath bald communities. Potential sites of phytotoxin origin, transport, transformation, and residence were examined for one year to document the biochemical dynamics of each bald. Statistical analyses were conducted between the test cases to identify those mechanisms that could contribute to the maintenance, stability, and persistence of the communities.

The implications of allelopathy in stability and succession theory were examined for both general and specific cases. The dynamics of the two test cases are explored in light of the recent changes in succession theory.

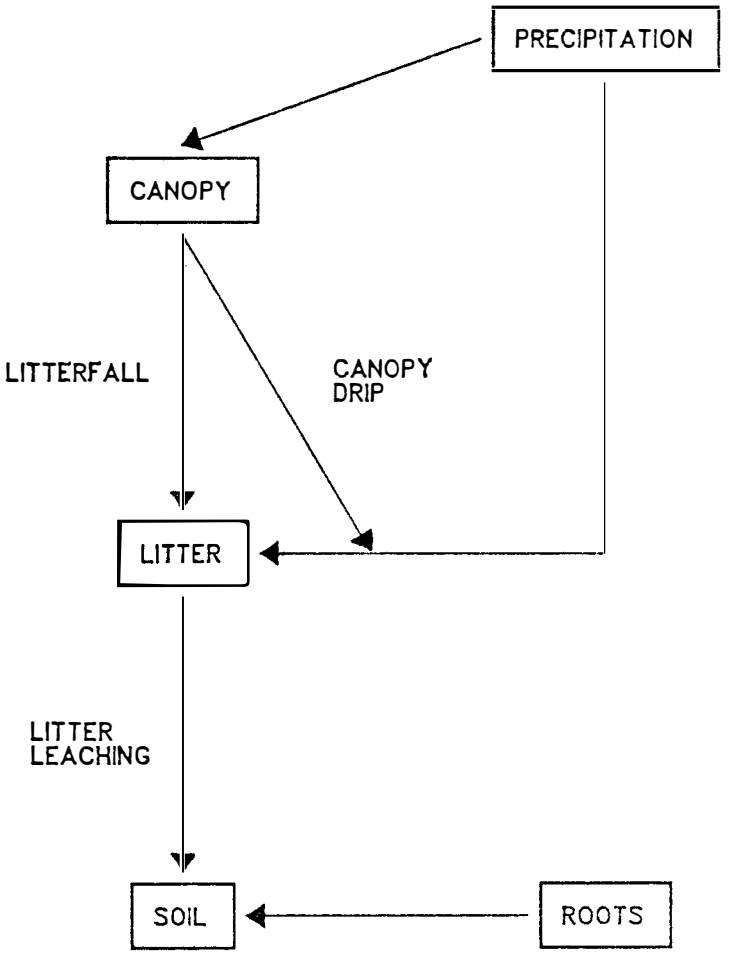

Figure 1. Conceptual model of potential phytotoxin sources, transport mechanisms, and locations of allelopathic interference. This model includes only those components selected for this investigation.

CHAPTER II

ALLELOPATHY AND COMMUNITY STABILITY

The relationship between allelopathy and stability in plant communities has been explored by Muller (1969, 1974) and Whittaker (1970, 1975). Allelopathy was described as a biochemical advantage that enables a species or community of accommodating species to attain and sustain dominance over potential competitors. By diminishing the potential for invasion and establishment, allelopathy can contribute to the stability of the plant community. The concept of community stability is interpreted here in the broader context of succession and climax theory. Thus, stability is considered a homeostatic state that emphasizes maintenance of a static or equilibrium condition.

The static approach to stability has been criticized for its inability to describe transient behavior of ecological systems that are not near equilibrium (Holling 1973). Recent approaches have been proposed that consider stability as a characteristic of the dynamic properties of an ecosystem. These dynamic alternatives attempt to define system stability by mathematical analysis of ecosystem models (Van Voris 1976).

Lack of a generally recognized definition of ecological stability has resulted in many different interpretations

of the term (Van Voris 1976). To avoid some of the difficulties associated with the static approach, the contemporary language of systems will be used to describe behavior of heath balds. Systems language is more rigorous and comprehensive than classical language and should provide a better instrument to explain concepts of stability.

Holling's (1973) definition of stability is "the ability of a system to return to an equilibrium state following a temporary disturbance." The region within which equilibrium occurs has been termed by him as the domain of attraction. In his definition, stability is defined as a property of the system and the degree of fluctuation around specific states, the result.

Holling (1973) also proposed another measure of ecosystem behavior, the property of resilience, that can contribute to the interpretation of stability. Resilience was defined as the ability of a system to absorb change and disturbance while still maintaining the same relationships between populations or state variables, and still persist. In his definition, resilience is defined as a property of the system with persistence being the result.

It is not the intent of this investigation to develop a mathematical model describing the role of allelopathic interference in the stability and persistence of southern Appalachian heath balds. Rather, terminology from dynamic stability concepts will be used to examine the relationships between allelopathy and ecosystem behavior.

CHAPTER III

ALLELOPATHIC EXTRA-METABOLITES FROM *KALMIA* AND *RHODODENDRON*

Historical records of western civilization afford numerous references to the toxic nature of the Ericaceae. Azaleas are noted for their deleterious effect on human health and laurels are known as toxic forages.

Descriptions of ericaceous toxicity can be traced to antiquity (Leach 1972) via the writings of Pliny (301 B.C.), Strabo (66 B.C.), and Xenophon (401 B.C.). One of the earliest and most lucid accounts of rhododendron toxicity can be found in the *Anabasis*, Bk. IV of Xenophon. The subjects were 10,000 Greek soldiers-of-fortune encamped near Trebizond on the Black Sea coast of Turkey. The following is a portion of this chronicle:

> As there were a great many bee-hives (in the surrounding villages), the soldiers did not spare the honey. They were taken with a vomiting and purging, attended by a delirium, so that the least affected seemed like men drunk, and others like mad men, or people on the point of death. The earth was strewed with bodies, as after a battle; not a person, however, died, and the disorder ceased the next day, about the same hour that it began. On the third and fourth days, the soldiers rose, but in the condition people are in after taking a strong potion (Barton 1802).

Accounts of North American origin prove equally enlightening:

> The kalmia latifolia, known in the United States by the name of laurel, great-laurel, wintergreen,

> spoon-haunch, spoon-wood, etc. is also poison. Its leaves, indeed, are eaten, with impunity, by the deer, and by the round-horned elk. But they are poisonous to sheep, to horned cattle and to horses. In the former of these animals, they produce convulsions, foaming at the mouth, and death (Barton 1802).

The potential adverse biological effects posed by members of the Ericaceae resulted in numerous analytical investigations. A single compound, thought to be the characteristic toxin of the order, has been isolated and identified. The compound has been assigned several names with acetylandromedol (Tallent et al. 1957), andromedotoxin (Wood et al. 1954), and grayanotoxin (Kakisawa et al. 1965) among the most common. For the purpose of this discussion, the term andromedotoxin is preferred. Structural analyses of andromedotoxin indicate a terpenoid compound, specifically, a toxic diterpene (Harborne 1973).

Biochemical surveys of the genera Kalmia and Rhododendron reveal other compounds that may produce adverse biological effects. Both genera contain representatives of such important chemical groups as phenols and phenolic acids, terpenoids and steroids, and toxic glycosides.

Within the phenolic grouping gallic acid (Rice 1965), hydroquinone (Chou and Muller 1972), and quercetin (Grümmer 1961) are recognized phytotoxins. The terpenoid and steroid group is represented by β-caryophyllene (Grümmer 1961), 2-pinene (Muller and Muller 1964), camphene (Muller and Muller 1964), α-phellandrene (del Moral and Muller 1970),

and limonene (Asplund 1968). Glycosides with demonstrated toxicity or precursors to phytotoxins include arbutin (Winter 1961) and phloridzin (Borner 1959). Other reported compounds of undetermined phytotoxicity include piperine, ursolic acid, and pyrocatechol (Merck Index 1968).

The existence of potential and demonstrated phytotoxins in species of Kalmia and Rhododendron suggests the capacity for allelopathic interference in these genera.

CHAPTER IV

SITE DESCRIPTION

I. LOCATION AND TOPOGRAPHY

The heath bald communities selected for investigation occur within the southern section of the Blue Ridge Province of the Appalachian Highlands (Fenneman 1938) in the Balsam Mountains of Haywood County, North Carolina. The communities are adjacent and located on a southwestward sloping leader of Waterrock Knob (mountain), at location 35°28'N - W83°8'30". The ridge is cut in half upslope by the Blue Ridge Parkway at mile 352.3. The balds occur at elevations between 1675 and 1700 m (5500 to 5600 ft). Slopes range from 30 to 60 percent over much of the area with steepness decreasing near the crest.

The two heath balds were designated sites A and B. Site A occupied a position directly upslope from B. The identity of site A was perceivable for 100 m along the crest of the ridge, for 50 m down the south-facing slope, and for 80 m down the north-facing slope. Site B was clearly identifiable for 200 m along the crest and for 100 m down the south-facing slope; the bald did not extend beyond the crest. A zone of integration, approximately 20 m wide, separated the two balds and was distinguishable by its heterogeneous assemblage of dominants from both communities.

II. CLIMATE

Employing the 1948 Thornthwaite climatic classification scheme, the Waterrock Knob vicinity at elevations between 1600 and 1800 m may be categorized as microthermal perhumid. At elevations of 1524 m in the neighboring and more thoroughly investigated Great Smoky Mountains, Shanks (1954) classified the climate as prehumid.

The climate of the region (including the Great Smoky Mountains and the Balsam Mountains) is thought to be influenced by different weather patterns in each of the four seasons (Stephens 1969). Seasonal precipitation patterns are characterized by maxima in late winter-early spring with a secondary peak in July. Minima occur in the autumn, especially during the month of October, with a secondary minimum in the month of May (Stephens 1969 and Weaver 1972).

Precipitation measurements were taken on-site. Three collectors were installed at random along the crest of site B. Each collector consisted of a 15 cm diameter catchment suspended above the canopy and connected to a buried storage reservoir. At two-week intervals, the reservoir volume was measured and a 150 ml subsample taken. The average monthly precipitation of all collectors is presented in Table 1.

Precipitation on-site and in the vicinity of the study areas was found to be both ample and well distributed during the course of the investigation. Precipitation data gathered

TABLE 1

MONTHLY AND ANNUAL PRECIPITATION RECORDED ON SITE AND AT TVA STATION 190, HAYWOOD GAP, NORTH CAROLINA FROM FEBRUARY 1973 THROUGH JANUARY 1974[a]

Month	On Site (cm)	Haywood Gap (cm)
February (1973)	27.8	11.7
March	21.8	39.6
April	29.1	16.6
May	25.8	27.2
June	18.1	19.4
July	9.2	9.5
August	9.2	5.9
September	8.8	9.4
October	5.4	7.7
November	19.6	26.3
December	25.3	28.3
January (1974)	23.6	24.5
Total	223.7	226.1

[a]Site data represent an average of three collectors.

on-site approximate the values reported for the Tennessee Valley Authority (TVA) monitoring station at Haywood Gap, North Carolina (Station No. 190). Comparisons of these data are available in Table 1. Thirty-nine years of data from the TVA station indicate annual average precipitation was 195.4 cm. During the history of the TVA operation, an annual precipitation maximum of 287.8 cm was recorded in 1957 and a minimum of 116.6 cm noted in 1941. Snowfall data were not available from the TVA station, but studies of similar elevations in the Great Smoky Mountains indicate values of 25-26 days per year of snowfall may be reasonable (Stephens 1969). From the same study, the greatest number of snow days occurred during March with snows being recorded as early as October and as late as April. Snow cover was reported to persist for approximately 50 days per year. In the Waterrock Knob area, snow accumulations were noted on six occasions during the study period. On only one occasion was accumulation greater than 10 cm.

Cursory temperature measurements were taken at each site with these data presented in Table 2. The on-site data and information obtained from the TVA station indicate that the summer months are cool and the winter months are relatively cold but not severe. Temperature data supplied by the National Oceanic and Atmospheric Administration (NOAA 1973) indicate that mean annual temperature ranges from 12-15° C at this general location and elevation.

TABLE 2

MAXIMUM AND MINIMUM AIR TEMPERATURES BENEATH TWO HEATH BALD CANOPIES[a]

Month	Location			
	Site A		Site B	
	Maximum	Minimum	Maximum	Minimum
February (1973)	-	-	-	-
	6	-13	11	-13
March	11	-2	17	-11
	11	-11	19	-10
April	12	-3	17	2
	12	-11	12	-11
May	18	-4	20	-4
	17	0	22	-2
June	17	8	17	4
	20	12	21	11
July	22	8	30	11
	21	13	30	11
	20	13	29	12
August	20	13	28	13
	18	11	26	9
September	21	13	31	12
	19	7	27	7
October	17	11	26	10
	16	1	25	0
November	15	-3	21	0
	11	-11	17	-2
December	12	-7	18	-8
	9	-14	10	-15
January (1974)	11	-4	8	-7
	10	-8	14	3

[a]Values are reported in °C at sample intervals of two weeks.

III. GEOLOGY

Most of the geologic formations in Haywood County, North Carolina have been described as being Cambrian or older (Goldston et al. 1954). Carolina gneiss is the oldest of all the formations in the region and the one that underlies the study sites. This formation has received recent investigation by Hadley and Goldsmith (1963), who concluded that it has undergone metamorphism and invasion by granitic materials during both the Precambrian and the later Paleozoic periods. The formation has been described as consisting of a heterogeneous assemblage of layered micaceous and hornblendic gneisses, mica schist, and amphibolite (Hadley and Goldsmith 1963). Additional distinctions include numerous faults and joints (Olsen 1946) and numerous enclosed bodies of intrusive, fine-grained granitoid materials (Keith 1907).

IV. SOILS

Waterrock Knob area has been mapped and described as a region of stony mountain uplands containing predominantly complexes of Porters and Ramsey soils, with possibility of Burton at the highest elevations (Goldston et al. 1954). The presence of Ramsey soils at high elevations in Balsam Mountains has been questioned by Weaver (1972), who contends that shale, quartzite, sandstone, or conglomerate parent materials are not known at these elevations.

Porters soils, developed from granite, gneiss, and schist, usually produce brown or dark-brown surface soil (A horizon) and a brown to yellowish-brown relatively open and permeable subsoil (B horizon). Relief ranges from hilly to very steep (30-60% slope) with numerous large angular rock fragments and many bedrock outcrops.

Burton soil is distinguishable from Porters and Ramsey soils by its dark-gray, almost black A horizon. The B horizon is light yellow-brown friable clay loam or loam. Most of Burton soils have been noted in the highest coves or on north-facing slopes and are usually associated with the Porters and Ramsey soils (Goldston et al. 1954). Relief ranges from strongly sloping to hilly (15-30% slope) with only occasional areas of steep slopes.

Soils beneath the heath balds consist predominantly of an organic mantle that lies almost directly on bedrock. Depth of this mantle varies from a few centimeters, adjacent to rock outcrops, to over one meter on the gentlest slopes. Porters and Burton soils are present in the forest communities surrounding the heath balds.

Soils similar to the above have been described in the Great Smoky Mountains and classified as Umbric Dystochrepts (Wolfe 1967). This recent classification corresponds to the previous nomenclature of Gray-Brown Podzolic soils (Goldston et al. 1954).

V. LAND USE HISTORY

The influence of human activity on high-elevation vegetation of the Balsam Mountains is thought to have been minimal prior to European settlement (Gersmehl 1970). Degradation of mountain lands began with selective logging and clearing for livestock pastures and progressed until much of the area was cutover or clearcut (Gersmehl 1970). As a result of intensive logging and frequent fire, 90% of the original southern Appalachian spruce-fir forest may have been destroyed by the early 1930's (Korstian 1937).

Forest depletion and the economic depression of the 1930's resulted in a major transition in land use practice (Gersmehl 1970). Large tracts of abandoned mountain lands were appropriated by the federal government and incorporated into the national forest network. During this period, land along the crest of the Balsam Mountains was acquired by the National Park Service for the Blue Ridge Parkway (Lord 1968).

Evidence of human activity was apparent only on site A. Cut stumps and occasional felled logs indicated activity. Deterioration of stumps and logs precluded estimates of date and purpose of cutting. It is not clear whether cutting was the result of early lumbering practices or the more recent clear-cutting required for the parkway.

VI. CATASTROPHIC EVENTS

Windfall, landslide, and fire are catastrophic factors considered influential in the initiation and maintenance of Appalachian heath balds (Cain 1930). Among these factors, fire was considered the most important. This perception was based upon indications of fire damage to root stocks and old stems and the presence of charcoal in heath bald soils. Landslides and windfall were events considered important predominantly in establishment and maintenance of high-elevation heath bald communities.

During the course of this investigation, both sites were examined for evidence of fire, landslide, and windfall activity. Small, denuded areas (< 20 m^2) along the ridge-crest of each site indicated localized fire damage from lightning strikes. Soil samples, caudices, and stems were investigated for signs of fire, but no charcoal was discovered.

Areas of potential and past landslide activity were located on south-facing slopes of both sites. Two separate landslides have occurred on site A and three on B. In all cases, activity appears to have originated in the balds and subsequently extended downslope. Fissures, extending through the soil to bedrock, were encountered on the south-facing slopes of each site. These crevices indicate slippage of the organic heath bald soil from bedrock and may represent

sites of future landslides. Revegetation was occurring along the margins and in rock crevices of the landslide areas. Woody invaders at these locations were predominantly Rhododendron and Vaccinium.

CHAPTER V

EXPERIMENTAL METHODS

Some methods have been used repeatedly in this investigation to study different aspects of the heath bald communities. Rather than continually duplicate these descriptions, the most frequently used bioassay and chemical techniques and analytical results have been compiled into this chapter. Additional methods, specific to a particular investigation, remain in their appropriate chapters.

Constraints on time and equipment made quantitative analyses of phytotoxins impractical in this investigation.

I. BIOASSAY TECHNIQUE

The fiberglass bioassay technique developed by Fuller (1977) was found to be the most suitable for determining seedling sensitivity to selected organic compounds and aqueous leachates. Pyrex wool was cut into 6 x 36 cm strips, rolled into bundles, and inserted into 2 x 7 cm snap-on plastic vials. Each bundle was irrigated with either distilled water (control), leachates, or laboratory stock solutions. Five pre-germinated seeds of either Abies fraseri, Betula lenta, or Tsuga canadensis were planted in a radial pattern between layers of the wool. Vials were

capped and seeds incubated in the dark at 25° C. Incubation period was 96 hours for Abies fraseri, 168 hours for Betula lenta, and 344 hours for Tsuga canadensis. All treatments were conducted in triplicate.

Aqueous Leachates

Soils from both heath balds and the adjacent Abies fraseri and Quercus borealis/Betula lenta forests were dried in a forced-air oven at 27° C for 48 hours. Samples were screened (2 mm mesh) to remove roots and stone fragments. Whole litter samples from both balds were also dried at 27° C for 48 hours before being ground through a Wiley Mill (2 mm mesh).

Ten g samples of soil or litter were added to 100 ml of boiling distilled water and allowed to steep for 36 hours. The mixture was filtered through Whatman No. 1 paper and the filtrate volume returned to 100 ml with distilled water.

Canopy drip leachates were obtained from collectors located on each heath bald. Samples were filtered through Whatman No. 1 paper and applied directly for bioassay studies.

Laboratory Standards

Analytical quality gallic acid, p-hydroxybenzoic acid, phloroglucinol, rhododendrol, and vanillic acid were obtained from commercial sources. A series of test solutions containing 1, 5, 10, and 50 mg/100 ml of distilled

was prepared for each compound. These laboratory solutions served as treatments for bioassay.

II. CHEMICAL TECHNIQUES

Samples of whole litter, leaf, root, soil, and litterfall materials were air-dried at 27° C for 48 hours before being either screened or ground to pass through a 2 mm mesh.

Extraction and Purification

Aqueous canopy drip samples were filtered with Whatman No. 1 paper. One hundred milliliter aliquots were removed from selected samples and treated with 2N HCl to rupture glysidic linkages and to polymerize phlobaphenes (Ribereau-Gayon 1972). Hydrolyzed samples were filtered repeatedly with Whatman No. 1 paper and reduced to less than 1 ml by low temperature evaporation. Samples were taken up in 95% ethanol.

Whole litter, leaf, root, and soil samples were subjected to Soxhlet extraction with 95% ethanol for 8 hours. Solvent volume was reduced to 5 ml and the crude extract allowed to cool to room temperature. The extracts were treated with 2N HCl, filtered with Whatman No. 1 paper, and reduced to 1 ml by low temperature evaporation. Samples were taken up in 95% ethanol.

Paper Chromatography

Paper chromatography was employed to separate and identify compounds extracted by ethanol from heath bald litters, litterfall components, canopy drip, roots, and soil. Descending chromatography was performed on sheets of Whatman No. 1 paper. Three separate solvent systems were selected to provide the maximum resolution of phenolic compounds. The first system was composed of isopropanol-acetic acid-water (Heftmann 1961), the second of butanol-acetic acid-water (Rice and Pancholy 1974), and the third of benzene-ammonia-water (Ibrahim and Towers 1960). Chromatographs were examined in ultraviolet light, with and without ammonia vapor treatment, and reactions of the different compounds with diazotized p-nitraniline (Ribereau-Gayon 1972), 2N Na_2CO_3 (Heftmann 1961), and 1% $FeCl_3$ (Ibrahin and Towers 1960). Color reactions and R_f values observed on the chromatographs of laboratory standards are presented in Table 3.

Gas Chromatography

Gas chromatography was used to confirm the identification of phenolic compounds obtained by paper chromatographic analysis and for identification of terpenoid compounds. A Perkin Elmer Model 3920 gas chromatograph, equipped with flame ionization detectors, flow regulators, and temperature programmer, was used to perform the analyses. Instrument output was recorded graphically by a Perkin Elmer Model 023

TABLE 3

R_f VALUES AND COLOR REACTIONS OF LABORATORY PHENOLS

Compound	Rf's on Whatman No. 1[a]			UV Fluorescence		Color[b]		
	BAW	PAW	BeAW	$-NH_3$	$+NH_3$	p-Nit.	Na_2CO_3	$FeCl_3$
Caffeic Acid	.78	.57	.82	bl	nc	br	gry	dgr
Catechol	.93	.73	.84	n	n	gry	pur.gry	blk
Chlorogenic Acid	.49	.63	.76	bl	gr	br	pur	bl
Ferulic Acid	.84	.61	.79	bl.viol	bl.gr	pk	bl	n
Gallic Acid	.67	.51	.30	yel	nc	yel	br	gr
Gentisic Acid	.79	.64	.53	bl	nc	gry	nc	bl.viol
p-Hydrocinnamic Acid	.84	.68	.86	n	n	yel.br	bl	org
Hydroquinone	.84	.71	.74	n	n	yel	red	-
p-Hydroxybenzoic Acid	.87	.55	.77	n	n	red	nc	yel
Kaempferol	.63	.79	.90	yel	nc	yel.br	nc	bl
Phloridzin	.91	.76	.49	yel	nc	yel.br	nc	bl
Phloroglucinol	.70	.61	-	n	bl	yel.br	nc	gry
Protocatechuic Acid	.78	-	.78	n	n	yel	br	bl.gr
Quercetin	.69	.57	.77	yel	yel	yel	nc	bl.gr
Vanillic Acid	.92	.60	.86	n	n	yel	viol	br

[a]Refer to text for description of solvent systems. R_f values represent the average of three runs.

[b]Colors: n = none, nc = no change, bl = blue, blk = black, br = brown, gr = green, gry = grey, org = orange, pk = pink, pur = purple, r = red, viol = violet, yel = yellow.

strip chart recorder, and the area under each peak automatically computed by a Perkin Elmer Model M-2 calculating integrator.

A 6 ft x 0.125 in O.D. glass column packed with 3% OV-17 on Chromosorb Q, 100/200 mesh, was used to separate both phenolic and terpenoid compounds. Instrument parameters were: column temperature programmed from 150° C (2 min hold) to 250° C (4 min hold) at a linear rate of increase of 32° C/min; inlet temperature at 250° C; detector temperature at 300° C; and nitrogen carrier gas flow rate of 70 ml/min. The column was baked out overnight at 280° C and gave a constant, low level baseline at the most sensitive settings. All sample volumes were 1 µl.

All laboratory standards were subjected to extraction, hydrolysis, and purification procedures. Treated standards were chromatographed for evidence of decomposition products. Retention times of laboratory standards were recorded relative to p-cymene (internal standard) to allow for minor variations in carrier gas flow rate. Retention times for standards are presented in Table 4.

TABLE 4

RELATIVE RETENTION VALUES OF PHENOLIC AND TERPENOID COMPOUNDS WITH RESPECT TO AN INTERNAL STANDARD

	Compounds		Column 3% OV-17	
I.	Terpenoid Compounds			
	Camphene		0.77	
	β-Caryophyllene		3.80	
	Limonene		0.93	
	α-Phellandrene		0.88	
	2-Pinene		1.03	
II.	Phenolic Compounds			
	Caffeic Acid		5.13	
	Catechol		1.68	
	Gallic Acid		6.13	
	Gentisic Acid		3.35	
	p-Hydrocinnamic Acid		1.75	
	Hydroquinone		2.95	
	p-Hydroxybenzoic Acid		7.38	
	Phloroglucinol		7.73	
	Protocatechuic Acid		1.65	
	Rhododendrol		6.63	
	Vanillic Acid		7.10	
III.	Internal Standard			
	p-cymene		1.00	
IV.	Operating Conditions			
	Carrier gas flow-rate	(ml/min)	70	
	Column temperature	(°C)	150	(initial)
	Injector temperature	(°C)	250	
	Interface temperature	(°C)	300	
	Column length	(ft)	6	

CHAPTER VI

FLORISTIC AND VEGETATIONAL SURVEY

Floristic descriptions of southern Appalachian heath balds have been published by Cain (1930), Brown (1941), and Whittaker (1956, 1963). They indicate that despite apparent physiognomic similarity, the presence and relative abundance of species could differ significantly among heath balds. Variability was attributed to the intensity and combination of such influences as climate and edaphic factors, catastrophic events, contiguous forest associates, and land management practices.

Few attempts have been made to categorize or classify heath balds. Cain (1930) proposed to group balds by altitude and adjacent forest type, Brown (1941) by species frequency and coverage, and Whittaker (1963) chose to distinguish them by major dominants.

Heath balds of the Balsam Mountains have not received the same degree of investigation or description as those of Roan Mountain and the Great Smoky Mountains. A lack of descriptive literature and general uncertainties about their composition made imperative an investigation of each site. A floristic and vegetational survey was conducted at both sites to describe each.

I. MATERIALS AND METHODS

Due to terrain, profusion of stems, and shrub habit a belt transect sampling technique was selected as the survey method (Brown 1941). Transects were surveyed both parallel and perpendicular to the ridge crest, along the longest axis of each site. Counts were made on stems taller than 0.5 m which occurred in a corridor 1.0 m on either side of the line.

Scientific nomenclature follows Gray's Manual of Botany (Fernald 1950).

II. RESULTS AND CONCLUSIONS

Survey results are presented in Table 5, expressed as stems per hectare. Rhododendron maximum was found to be predominant on both slopes of site A, with Vaccinium spp. ranking next. On the north slope, Rhododendron constituted approximately 93% of the stems, and on the south slope, 73%. The difference is attributable to more Vaccinium (x4), Picea rubens (x5), and unidentified shrub species. Although both slopes contained the same number of Rhododendron stems, the north slope produced approximately 20% fewer total stems per hectare.

Site B was dominated by Rhododendron catawbiense with Kalmia latifolia and Vaccinium spp. constituting the majority of remaining species. Total number of stems per hectare was substantially higher for site B than for either slope of A.

TABLE 5

SPECIES COMPOSITION AND REPRESENTATION WITHIN HEATH BALD COMMUNITIES

Location	Species	Stems Per Hectare	Percent of Total
Site A, north slope	*Betula lenta*	136	.51
	Picea rubens	182	.68
	Prunus serotina	68	.25
	Rhododendron maximum	25,117	93.17
	Vaccinium spp.	1,228	4.55
	Unidentified species	227	.84
	Total	26,958	100.00
Site A, south slope	*Abies fraseri*	134	.38
	Betula lenta	167	.48
	Kalmia latifolia	34	.10
	Picea rubens	1,167	3.34
	Rhododendron maximum	25,564	73.11
	Vaccinium spp.	5,666	16.20
	Unidentified species	2,233	6.39
	Total	34,965	100.00
Site B	*Abies fraseri*	17	.03
	Betula lenta	166	.33
	Kalmia latifolia	4,565	9.08
	Picea rubens	166	.33
	Prunus serotina	67	.13
	Rhododendron catawbiense	38,068	75.71
	Vaccinium spp.	6,697	13.32
	Unidentified species	533	1.06
	Total	50,279	99.97

Differences are ascribed to an increase in the number of Rhododendron and Kalmia stems.

Comparison of survey data with available literature indicates that the study sites are floristically similar to previously described southern Appalachian heath bald communities. Site A has been referred to in Chapter I as a heath bald, but this community resembles Whittaker's (1963) description of a spruce-rhododendron forest heath. The major differences between descriptions of site A and the forest heath are the dominance of Rhododendron maximum instead of Rhododendron catawbiense at site A and the absence of a closed tree stratum at A. Both descriptions contain a significant number of Picea rubens stems, reflecting establishment of this canopy competitor. Continued success of Picea at site A would eventually result in Whittaker's spruce-rhododendron forest heath community.

Survey data of site B are similar to the mixed heath bald communities of Whittaker (1963). The mixed heath balds occur in the Great Smoky Mountains and are regarded by Whittaker as central to the heath complex of the region. These balds occupy altitudes between 1,370 and 1,700 m, possess a 1-3 m high closed shrub canopy, and are dominated by Rhododendron catawbiense and Kalmia latifolia. Frequent associates include Vaccinium constablaei, Pyrus melanocarpa, and Viburnum cassinoides, with Rhododendron maximum, Rhododendron carolinianum, Clethra acuminata, and Gaylussacia

baccata also reported (Whittaker 1963). These characteristics adequately describe the heath bald community of site B.

CHAPTER VII

HEATH CANOPY

Phytotoxins have been isolated from flowers, leaves, stems, and small branches of Kalmia latifolia, Rhododendron catawbiense, and Rhododendron maximum (Wood et al. 1954 and Tallent et al. 1957). Presence of phytotoxins in canopy components of heath bald dominants indicates a potential for allelopathic interference.

The importance of the heath bald canopy could also be increased by its evergreen habit. Continual canopy presence could provide a residual input of phytotoxins to the litter and soil. During the winter, temperature extremes could injure leaves and result in release of phytotoxins.

Age is another factor that may contribute to the importance of the heath canopy. Leaves of Kalmia latifolia, Rhododendron catawbiense, and Rhododendron maximum may be retained from 2-6 years. During this period, leaf permeability and subsequent phytotoxin loss may be increased by solar radiation, temperature extremes, disease, and insect predation.

The mere presence of canopy toxins does not confirm allelopathic interference. Phytotoxins must be transferred effectively from the plant to invading representatives of competitive species. Performance of this function requires both viable release and transport mechanisms. Synopses of

reported mechanisms of canopy release and transport are available in the recent texts of Rice (1974) and Sondheimer and Simeone (1970).

The schlerophyllous vegetation of the heath balds suggests two probable release and conveyance mechanisms. Canopy drip could provide a continuous source of phytotoxins from the evergreen canopy. Litterfall could provide phytotoxins through the year and also during seasonal leaf drop. For these reasons, canopy drip and litterfall were investigated at each site for the presence of phytotoxins.

I. CANOPY DRIP

The ability of dew, fog, mist, and rain to leach metabolites from above-ground plant parts is well-documented and reviewed (Tukey 1970). A variety of chemicals including inorganic and organic compounds, macro- and micro-elements, essential minerals, and growth-regulating substances have been detected in canopy leachates (Tukey and Morgan 1964).

Loss of canopy metabolites has potential ecological implications in the distribution (Arens 1934), structure (Bonner 1950), and function (Whittaker 1975) of plant communities. The effectiveness of canopy metabolites in determining understory species representation is a relative measure of its community level importance. Leachate influence on understory vegetation that reduces biological competition can be interpreted as allelopathic interference.

A monitoring program was initiated at both balds to qualitatively define phytotoxin presence in canopy drip. Seasonal allelopathic potential of canopy drip was assessed at monthly intervals.

Materials and Methods

Three canopy drip collectors were installed on each slope of site A and B. Each collector consisted of a 15 cm diameter catchment suspended 20 cm above the soil and connected to a buried reservoir.

All collectors were serviced at two-week intervals for one year. Fluid volumes were recorded and 150 ml samples taken. Phytotoxins were extracted and identified from selected monthly samples by the procedures described in Chapter V. Combined monthly samples were used in bioassay with *Abies fraseri*, *Betula lenta*, and *Tsuga canadensis* as test species (Chapter V, pages 19-20).

A one-way analysis of variance with equal sample sizes was performed on the canopy drip test data of each test species (Sokal and Rohlf 1969). All treatments were performed in triplicate.

Results and Conclusions

The chemical analyses indicated the presence of hydroquinone, p-hydroxybenzoic acid, and rhododendrol in the canopy drip of both heath balds. Table 6 presents monthly tabulations of the compounds detected at both

TABLE 6

DETECTION OF PHENOLIC COMPOUNDS IN MONTHLY CANOPY DRIP SAMPLES FROM TWO HEATH BALDS

Location	Compound	Date[a] Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan. (1974)
Site A	Hydroquinone	-	-	-	-	+	+	+	+	-	-	-	-
	p-Hydroxybenzoic Acid	-	-	-	-	+	+	+	+	-	-	-	-
	Rhododendrol	+	+	+	+	+	+	+	+	+	+	+	+
Site B	Hydroquinone	-	-	-	-	+	+	+	+	-	-	-	-
	p-Hydroxybenzoic Acid	-	-	-	-	+	+	+	+	-	-	-	-
	Rhododendrol	+	+	+	+	+	+	+	+	+	+	+	+

[a](-) Compound not detected in cample.
(+) Compound detected in sample.

balds. Rhododendrol was the only compound that was detected every month, while the remaining compounds were restricted to the summer months (June-September).

Statistical analysis of the bioassay data indicated that radicle growth did not differ significantly among monthly watering treatments for any test species.

Although three phytotoxins were isolated and identified from the canopy drip of both heath balds, concentrations were insufficient to significantly affect radicle growth of the three test species. Lack of detectable inhibition, however, does not totally exclude canopy drip as a viable component in the establishment of allelopathic interference. Low-level phytotoxin contributions from the canopy may eventually accumulate to toxic concentrations in litter or soil. Concurrently, these three may accumulate with other compounds to form an effective suite of phytotoxins whose synergism results in allelopathic interference.

II. LITTERFALL

Phytotoxins are transferred directly from the canopy to the soil surface in litterfall. Bark, branches, leaves, reproductive structures, and tissue fragments are potential transport vehicles. The evergreen habit of the heath bald canopies temporally expands the opportunity for allelopathic interference. Lack of an apparent peak in litterfall emphasizes canopy presence and indicates the need for

investigation of this aerial stratum. Date, rate, and composition of litterfall are major criteria for evaluation of this potential transport mechanism.

A sampling program to monitor the rate and composition of litterfall was initiated on both heath balds. Selected litterfall components were chemically analyzed to qualitatively define phytotoxin presence at each location.

Materials and Methods

Six litterfall collection bins were randomly located on each bald. Each bin consisted of a one bushel basket, 45.5 cm in diameter, with a fine nylon mesh cloth bottom. All bins were suspended 20 cm above the soil and leveled. Bins were emptied monthly. Individual collections were sorted into leaves and bud scales, flowers and seeds, branches (less than 45.5 cm in length), and stems (greater than 45.5 cm in length). All materials were air-dried, weighed, and their weights compiled by month and heath bald. Selected components were removed at random for chemical extraction, purification, and identification of phytotoxins (Chapter V, pages 21-25).

Three 1 x 5 m rectangular plots were laid out on each slope of site A and on site B. These areas were designed to collect woody materials that exceeded the diameter of the collection bins. Litter was removed to the A_1 horizon in all areas. After one calendar year, all woody material greater than 45.5 cm in length was removed. Woody material

was air-dried, weighed, recorded, and discarded.

Results and Conclusions

Results of the litterfall investigation are presented in Tables 7 and 8. Data indicate that Rhododendron leaves constitute the largest annual contribution to litter with 56% at site A and 62% at B. Leaves of both species were shed continually through the year with most falling between June and October. Early summer losses at both balds were apparently due to a flush of spring foliage that failed to survive mild drought (Table 1, page 11). Most leaf drop occurred in August on site A (39%) and in September on B (35%). These periods were distinguished by yellow leaves; no other collections contained yellow leaves.

Intact stems and branches were infrequently encountered in either the elevated or surface collectors. Dead wood remained in the canopy supported by surrounding shrubs. Standing dead wood was lost from the canopy by attrition. Wind appeared to be the major force that determined the loss of canopy dead wood. This contention is supported by collections for October, a month when storms and high winds (NOAA 1973) produced 36% of the annual wood deposition at site A and 22% at B.

Results of the chemical survey conducted on selected litterfall components of each bald are presented in Table 9 for leaves, flowers, and wood samples of Rhododendron maximum and catawbiense.

TABLE 7

MEAN MONTHLY LITTERFALL (KG/HA) AT SITE A

Components	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan. (1974)	Annual	Total
Leaves and Bud Scales														
Rhododendron maximum	44.6	93.2	62.4	51.3	193.0	415.3	1058.0	525.3	122.1	65.3	45.4	46.2		2722.1
Vaccinium spp.	0	0	.6	4.1	2.2	3.4	67.5	259.4	58.6	8.0	3.1	1.4		408.3
Flowers and Seeds	0	3.6	.7	2.1	22.3	3.3	10.1	22.3	16.7	12.4	3.5	0		97.0
Bark	15.9	5.1	1.4	25.6	2.1	1.4	2.3	2.2	75.2	19.1	58.7	16.9		225.9
Branches (≤ 45.5 cm in length)														
Rhododendron maximum	4.9	16.3	1.6	0	0	6.4	12.9	33.9	294.7	171.6	29.8	5.1		577.2
Vaccinium spp.	0	11.3	3.8	7.2	.5	2.7	0	21.6	26.5	3.0	9.5	1.4		87.5
Stems (> 45.5 cm in length)													231.6	231.6
Other	80.9	17.3	24.9	72.9	16.4	15.8	39.1	100.9	24.3	37.8	39.7	83.1		553.1
Total	146.3	146.8	95.4	163.2	236.5	448.3	1189.9	965.6	562.0	373.3	189.7	154.1	231.6	4902.7

TABLE 8

MEAN MONTHLY LITTERFALL (KG/HA) AT SITE B

Components	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan. (1974)	Annual	Total
Leaves and Bud Scales														
Kalmia latifolia	0	3.2	2.6	2.1	11.2	1.6	4.3	8.2	8.1	0	2.0	0		43.3
Rhododendron catawbiense	42.8	89.6	32.5	64.1	235.8	345.3	622.2	932.6	208.5	35.7	85.0	8.1		2702.2
Vaccinium spp.	.3	0	.3	14.0	2.9	4.7	36.6	2.5	323.5	21.1	5.1	.3		411.3
Flowers and Seeds	2.1	.1	.2	1.7	28.3	8.4	20.6	25.0	16.6	7.3	4.0	2.9		117.2
Bark	34.6	12.6	16.7	63.8	3.1	10.5	3.9	.3	30.9	8.8	33.1	55.5		273.8
Branches ($\leq$ 45.5 cm in length)														
Rhododendron catawbiense	1.3	1.4	44.7	0	.7	0	0	1.3	102.9	1.1	4.8	7.4		165.6
Vaccinium spp.	7.3	.8	1.7	7.1	0	0	.3	1.6	63.0	10.2	59.1	10.4		161.5
Stems (> 45.5 cm on length)													330.9	330.9
Other	10.3	8.3	6.5	13.9	4.4	6.9	18.6	24.1	27.2	13.4	3.3	14.5		151.4
Total	98.7	116.0	105.2	166.7	286.4	377.4	706.5	995.6	604.0	274.3	196.4	99.1	330.9	4357.2

TABLE 9

CHEMICAL SURVEY OF LITTERFALL COMPONENTS FROM *RHODODENDRON CATAWBIENSE* AND *R. MAXIMUM* HEATH BALDS

Components	Identified Compounds						
	Gallic Acid	Hydroquinone	p-Hydroxy-benzoic Acid	Phloroglu-cinol	Quercetin	Rhododendrol	Vanillic Acid
Leaves							
Yellow	+	+	+	+	+	+	+
Green	+	+	+	-	+	+	+
Flowers[a]	-	+	-	-	-	+	+
Wood[b]	-	-	+	-	-	+	+

[a]Includes seed and reproductive structures.

[b]Combination of bark and branchfall materials.

Seven phenolic compounds were isolated and identified from the litterfall components of each heath bald (Table 9). Rhododendrol and vanillic acid were detected in all samples. Hydroquinone and p-hydroxybenzoic acid were absent only from flower samples. Gallic acid, phloroglucinol, and quercetin were restricted to leaf samples.

The chemical survey confirmed that both heath bald species contribute phytotoxins to litter by loss of leaves, flowers, and woody materials. The pattern of phytotoxin presence in litterfall components is identical in the two Rhododendron species. Leaf tissues contained the largest number of phytotoxins, with flowers and wood providing fewer kinds of the same compounds. Comparison of chemical data from yellow and green leaves indicated an identical pattern of phytotoxins in the two species. Combination of litterfall and chemical information reveals a mechanism for continual influx of phytotoxins to litter. A major seasonal contribution from the canopy can be recognized in the fall as a result of leaf drop and branchfall. Continuous phytotoxin influx supported by a surge in the fall establishes the canopy layer as a viable force for the development and maintenance of allelopathic interference in the litter and soil.

CHAPTER VIII

HEATH LITTER

Phytotoxins and candidate toxins lost from the heath bald canopy in living, injured, and dead plant tissues have the capability to produce allelopathic interference in litter.

Regardless of original chemical composition, once deposited, these compounds enter the jurisdiction of prevailing abiotic and biotic forces in the litter. Compounds may be released directly into the environment by leaching or volatilization. Tissue destruction by macro- and microorganisms also releases phytotoxins to the environment.

While residing in litter, toxic and potentially toxic substances become involved in many complex interactions, syntheses, and transformations. Complex organic compounds are unstable in this new environment and decompose into less reactive daughter products. Microorganisms can also toxify innocuous compounds (Patrick 1971) and synthesize phytotoxins from plant residues (Norstadt and McCalla 1963). The interactions among these various abiotic and biotic forces may increase or reduce allelopathic interference in heath bald litter.

The intimate contact between heath litter and overwintering or germinating seed of woody competitors affords

an opportunity for expression of allelopathic interference. Phytotoxins in litter are capable of mobility and effective toxicity but are susceptible to transformation, degradation, and detoxification. Allelopathic success of phytotoxins is dependent upon maintaining a residual level of toxicity during the year. Without effective phytotoxin concentrations, allelopathy would be incomplete and identity of the heath balds could be lost.

Assessment of allelopathic potential in the litters of the two heath balds required a program to measure the presence of phytotoxins and the inhibitory effectiveness of the litters.

I. MATERIALS AND METHODS

A single 25 m^2 sampling location was established on each heath bald. Each area was cordoned off, and grab samples of whole litter were removed at two-week intervals for bioassay (Chapter V, pages 19-21) and chemical analysis (Chapter V, pages 21-25).

A two-way analysis of variance with replication was used to test differences in radicle growth of Abies fraseri, Betula lenta, and Tsuga canadensis germinating seeds subjected to different substrate treatments (Sokal and Rohlf 1969). Substrate treatments were aqueous leachates of litter samples taken from each heath bald (Chapter V, pages 19-21). All treatments were replicated three times.

II. RESULTS AND CONCLUSIONS

Results of the chemical survey of heath bald litters are presented in Table 10 for site A and in Table 11 for B. Two litter samples from each month were analyzed from each bald. The number of times a compound was detected in the samples from each location (frequency) is indicated in Tables 10 and 11. The seven phenolic compounds identified in Table 10 were detected at different periods through the year. The frequency of detection for gallic acid, hydroquinone, p-hydroxybenzoic acid, and rhododendrol increased from July through October. This change corresponds to an increase in litterfall during the same period. A similar comparison can be made at site B where gallic acid, p-hydroxybenzoic acid, and vanillic acid increased with litterfall. The period of maximum litterfall at each site was the same. The direct relationship between litterfall and presence of phenolics reveals that these compounds do not remain in the litter. Without a continuous influx of canopy material, phenolic compounds are rapidly lost from the litter. Loss may be attributed to leaching and microbial degradation. Phenolic compounds detected between November and June appear to be from new litter rather than residual toxicity.

Bioassays were conducted on aqueous leachates of monthly litter samples taken from sites A and B. Response of Abies fraseri seedlings to site A and B litter leachates

TABLE 10

CHEMICAL SURVEY OF LITTER FROM *RHODODENDRON MAXIMUM* BALD[a]

Sample Date	Identified Compounds[b]					
	Gallic Acid	Hydroquinone	p-Hydroxybenzoic Acid	Phloroglucinol	Rhododendrol	Vanillic Acid
Feb. (1973)	-	-	-	-	+	-
Mar.	-	+	-	+	-	+
Apr.	-	-	+	-	+	-
May	+	-	+	-	+	+
June	-	+	+	-	-	-
July	++	-	++	+	+	+
Aug.	++	+	++	++	++	++
Sept.	++	+	++	+	++	++
Oct.	++	+	++	-	++	-
Nov.	+	+	+	-	+	+
Dec.	-	-	-	+	-	+
Jan. (1974)	-	+	-	-	+	+

[a]Compounds extracted from litter and identified by methods described in Chapter V, pages 21-25.

[b](-) Compound not detected in either sample.
(+) Compound detected in one sample.
(++) Compound detected in two samples.

TABLE 11

CHEMICAL SURVEY OF LITTER FROM RHODODENDRON CATAWBIENSE BALD[a]

Sample Date	Identified Compounds[b]					
	Gallic Acid	Hydroquinone	p-Hydroxybenzoic Acid	Phloroglucinol	Rhododendrol	Vanillic Acid
Feb. (1973)	-	-	+	-	+	+
Mar.	-	-	-	-	-	-
Apr.	+	-	-	-	-	-
May	-	+	+	-	++	-
June	+	-	-	-	++	+
July	-	-	+	-	++	++
Aug.	+	+	++	+	++	++
Sept.	+	-	++	+	++	+
Oct.	+	+	++	-	++	+
Nov.	+	-	+	+	++	+
Dec.	-	-	+	-	+	-
Jan. (1974)	-	-	-	-	+	-

[a]Compounds extracted from litter and identified by methods described in Chapter V, pages 21-25.

[b](-) Compound not detected in either sample.
(+) Compound detected in one sample.
(++) Compound detected in two samples.

is illustrated in Figure 2. All leachates produced radicle inhibition in Abies. Statistical analysis indicated that variability in radicle inhibition does not differ significantly between site A and B litters; however, a highly significant difference ($P > 0.001$) was detected between monthly samples. Cyclical trends can be noted from the two data sets presented in Figure 2. Peak inhibition, occurring in the fall, is followed by a decline in the winter and spring and an increase in the summer. The inhibition pattern described for sites A and B resembles the monthly litterfall contribution of Rhododendron leaves at each site. Calculation of the product-moment correlation coefficient (r) between monthly Rhododendron leaf fall and percent radicle reduction in Abies fraseri produced values of 0.45 for site A and 0.18 for B. The correlation coefficients do not indicate a high association between leaf fall and percent inhibition at either site.

Results of the bioassays using Betula lenta as test material are presented in Figure 3 for sites A and B. Betula seedlings were found to be generally less sensitive to litter leachates than those of Abies. Despite the reduction in sensitivity, the seasonal inhibition pattern described for Abies also applies to Betula. Statistical analysis of the bioassay data indicates no significant difference in radicle inhibition between sites A and B litter treatments. As in the case of Abies, there was a highly significant

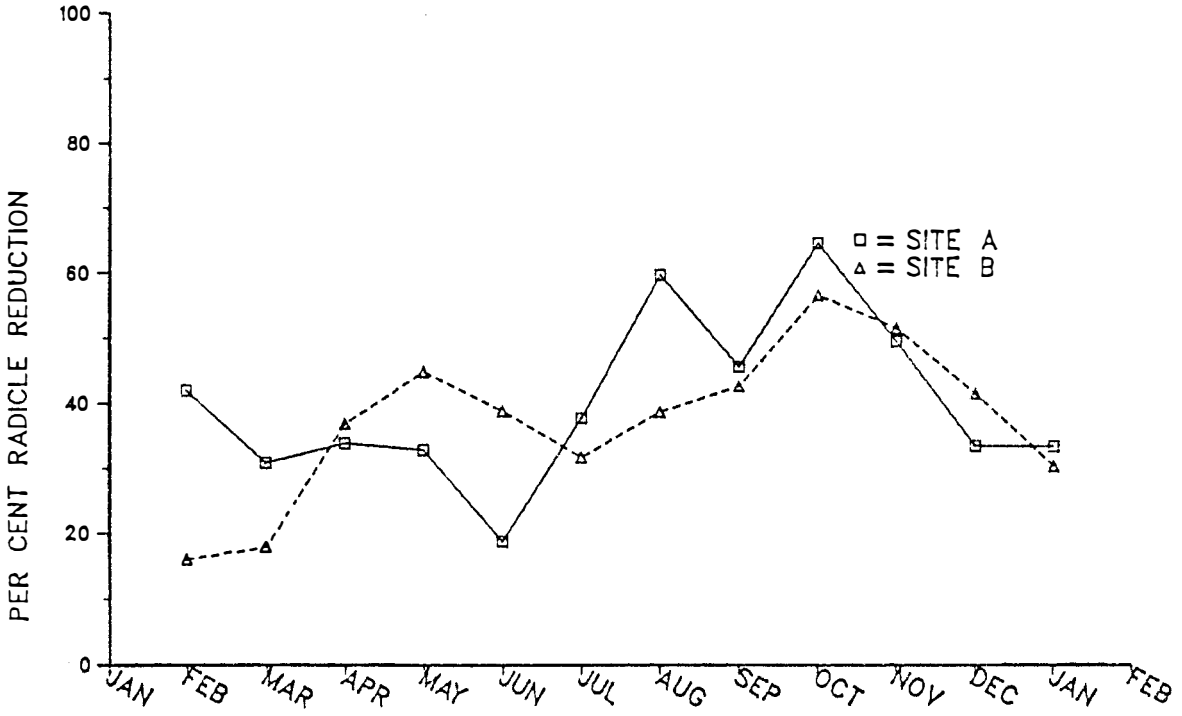

Figure 2. The effect of aqueous leachates of monthly litter samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds on radicle growth (expressed as percentage of control) in Abies fraseri.

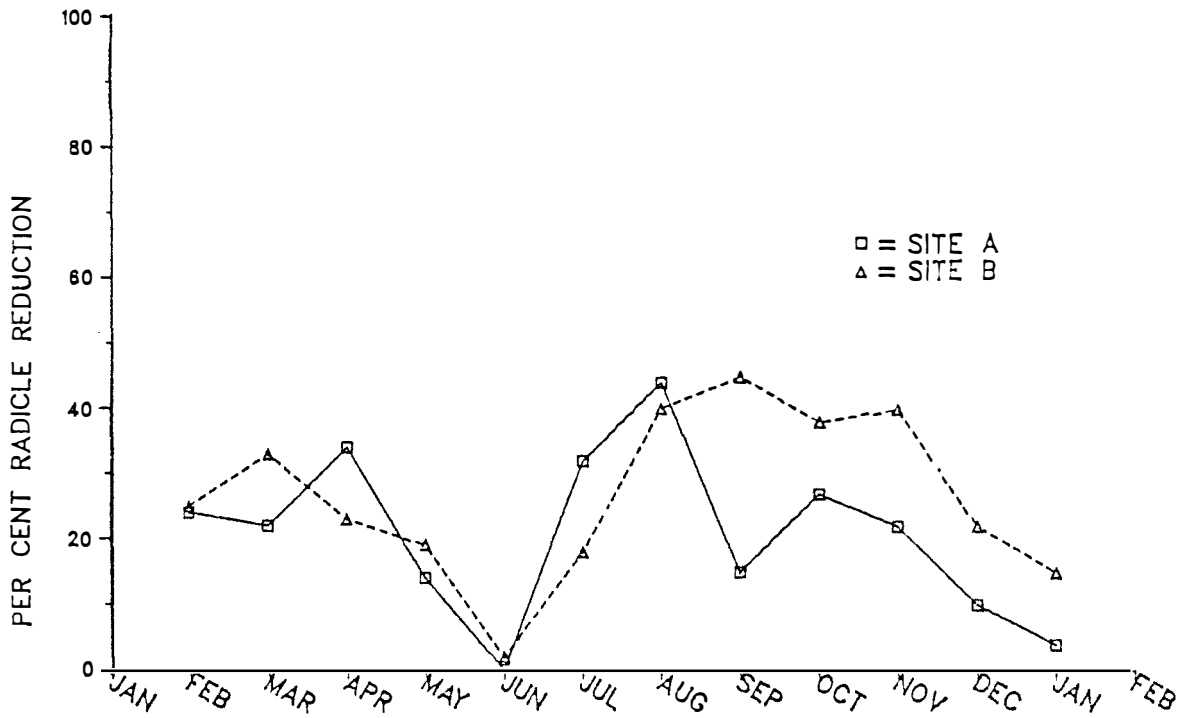

Figure 3. The effect of aqueous leachates of monthly litter samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds on radicle growth (expressed as percentage of control) in Betula lenta.

difference ($P > 0.001$) between monthly litter treatments of both sites. Correlation coefficients between monthly Rhododendron leaf fall and percent radicle reduction in Betula lenta are 0.53 for site A and 0.47 for B. Although these correlation coefficients are higher than those calculated for Abies, the r values are not large enough to indicate a high association between the variables.

The bioassays employing Tsuga canadensis yielded results that were similar to those of the other test species. Statistical analysis of the bioassay data indicate no significant difference between the litters of sites A and B in producing radicle reduction in Tsuga seedlings. As with other test species, the difference between monthly litter treatments was significant ($P > 0.001$). The Tsuga data indicated a distinct forward shift in the period of peak inhibition (Figure 4). At both sites, the period of peak inhibition began and declined a month earlier than for Abies and Betula. This shift did not produce a strong correlation between monthly Rhododendron leaf drop and percent radicle reduction of Tsuga at site A where $r = 0.43$. At site B, however, a coefficient of 0.79 indicated a strong association between the variables. Other than these differences, the inhibition pattern established for Tsuga at sites A and B corresponds to those described for the other test species.

The purpose of the investigation was to test for phytotoxins in the litter of two heath bald communities and

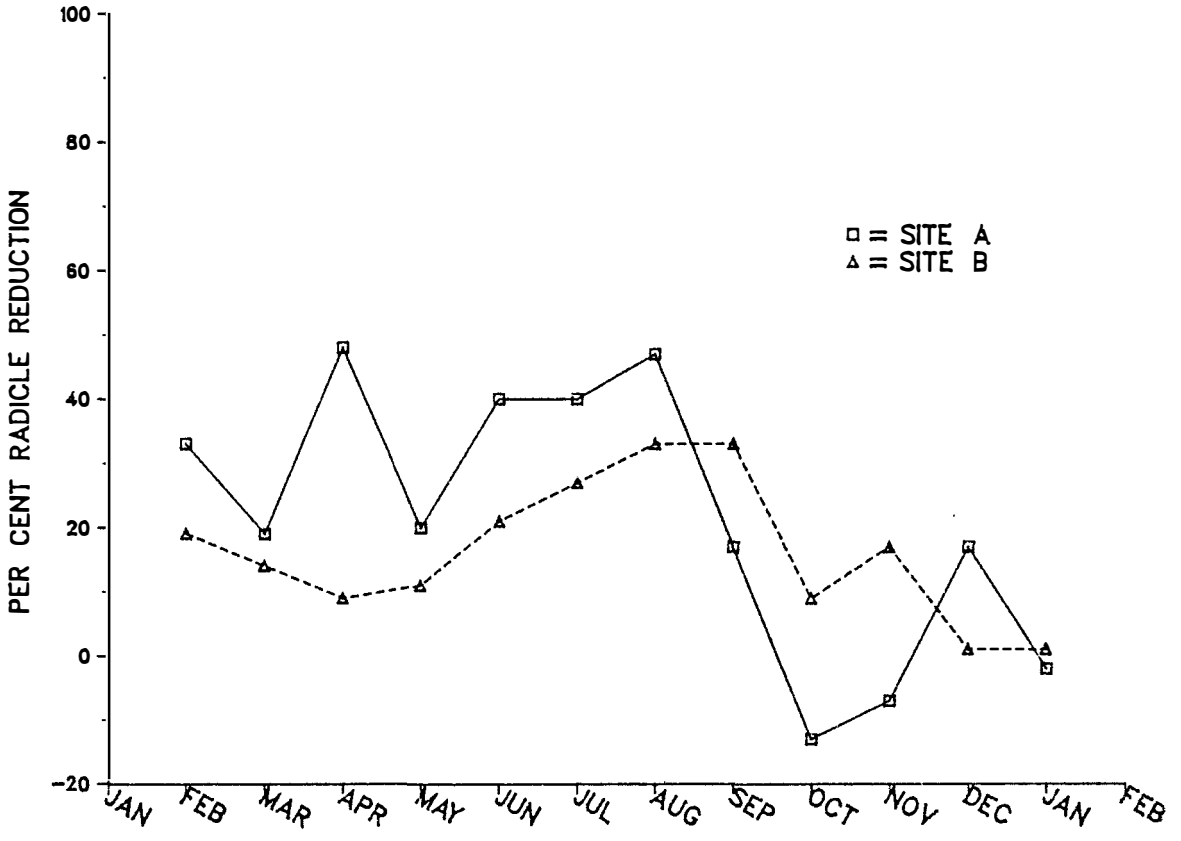

Figure 4. The effect of aqueous leachates of monthly litter samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds on radicle growth (expressed as percentage of control) in Tsuga canadensis.

subsequently to assess the allelopathic potential of these media. A suite of phytotoxic compounds was isolated and identified from both locations and the frequency of each compound established. The continued presence of those suites appears to be dependent upon continuous introduction of Rhododendron leaf material from the canopy. Without this influx, the phenolics are not retained in the litter.

Bioassays using aqueous litter leachates from sites A and B indicated a seasonal cycle of inhibition at both heath balds. Maximum inhibition occurred in the summer, declined in the late fall through winter, and increased in the spring.

The combination of chemical analyses and bioassays indicate the potential for allelopathic interference in the litter zones of each heath bald. The maximum inhibition occurred during the spring and summer months. Inhibition occurred the remainder of the year providing a deterrent to the overwintering seeds of woody competitors.

CHAPTER IX

HEATH RHIZOSPHERE

The importance of the soil has seldom been underestimated by investigators of allelopathic interference. The zone between litter and bedrock is the environment that can most thoroughly test the competitive capabilities of a species. Beyond the successful acquisition of water and nutrients, establishment and control of space is mandatory. Longevity and integrity of this space can contribute to the interspecific success of the species.

As in the canopy, numerous pathways are available for the production of allelopathic interference in soil. Soil can be affected externally by canopy and litter leachates (Tukey 1970) and internally by root exudates (Woods 1960) and decay products (Grümmer 1961). Accumulation of phytotoxins at the surface or at different depths can reduce the viability of buried seed (Evenari 1949) and produce a deterrent to successful establishment of competitive root systems (Woods 1960).

For these reasons, the presence of phytotoxins in heath bald roots and soil was investigated. Allelopathic potential of heath soils was examined by bioassay to define periods of maximum adverse effect to the germinating seed of woody competitors.

I. ROOT SYSTEMS

De Candolle (1832) was among the first of the modern scientists to suggest that root exudates from one species could adversely affect another in natural plant communities. Roots have routinely been investigated for phytotoxins since that time, and a variety of organic compounds (Woods 1960 and Winter 1961) and release mechanisms (Whittaker and Feeney 1971) have been identified.

Beyond initial toxicity, phytotoxicity can be enhanced by root system configuration. Root density and depth may provide a direct means of exerting allelopathic control in the soil. Phytotoxin release near the surface could thwart seed germination and establishment. At greater depths, invading roots and rhizomes could be excluded by root exudation, leaching, and decomposition.

The extent to which allelopathic interference can be expressed by the root systems of heath bald constituents was investigated. Studies were initiated to detect phytotoxins produced in different sized roots and to define their zones of greatest potential influence.

Materials and Methods

Soil depth was measured at 10 m intervals along transects through each site. Five locations were selected on each site for excavation of 0.5 x 0.5 m soil columns. Columns were removed in 20 cm segments. Segments were

washed over 2 mm screens and root material removed. Roots were sorted into five size classes, air dried, and weighed. Subsamples were taken from each size class for chemical extraction and identification of phytotoxins (Chapter V, pages 21-25).

Results and Conclusions

The dominant species on both sites exhibited extensive and complex root systems characterized by a deeply-seated rootstock (caudex). Caudices less than 10 cm in diameter occurred at or near the surface, while larger stocks were noted at all depths. Caudex diameters ranged from 5 to 50 cm. Taproots were absent from the caudices, leaving anchorage to enlarged secondary vertical roots. Lateral roots extended from the caudex to branch and rebranch at all depths. Masses of fibrous roots arose from lateral roots, rhizomes, and caudices, intertwining to produce a tightly woven root fabric in the first 40 cm of soil. Rhizomes also emerge from the caudex, extending horizontally at depths between 5 and 20 cm.

Table 12 presents the dry weight of living underground organs per hectare recovered from successive 20 cm soil depths. Total dry weight at each depth represents contributions from rhizomes and five size classes of roots. Density of underground organs was greatest in the first 20 cm sample of both sites. Forty-seven percent of the total weight recorded for site A occurred in this zone and 42% for site B.

TABLE 12

DEPTH DISTRIBUTION AND WEIGHT OF UNDERGROUND ORGANS IN TWO HEATH BALDS

Depth (cm)	Size Class[a]	Weight (10^3 kg/ha) 1	2	3	4	5	Total (10^3 kg/ha)
Site A							
0-20		8.7 (25%)[c]	5.1 (15%)	3.6 (10%)	7.4[b] (21%)	9.8[b] (28%)	34.6 (47%)[d]
21-40		8.3 (40%)	2.9 (14%)	3.3 (16%)	3.3 (16%)	3.0 (14%)	20.8 (28%)
41+		3.1 (17%)	1.0 (5%)	2.5 (14%)	9.3 (50%)	2.6 (14%)	18.5 (25%)
		-	-	-	-	-	-
		20.1 (27%)	9.0 (12%)	9.4 (13%)	20.0 (27%)	15.4 (21%)	73.9
Site B							
0-20		12.9 (49%)	7.9 (30%)	5.5[b] (21%)	--	--	26.3 (42%)
21-40		8.6 (35%)	4.8 (19%)	6.0 (24%)	5.5 (22%)	--	24.9 (40%)
41+		1.2 (10%)	0.2 (2%)	5.4 (47%)	4.7 (41%)	--	11.5 (18%)
		-	-	-	-		-
		22.7 (36%)	12.9 (21%)	16.9 (27%)	10.2 (16%)	--	62.7

[a]Class 1 - 0.1 to 1 mm; 2 - 1.1 to 5 mm; 3 - 5.1 to 10 mm; 4 - 10.1 to 50 mm; 5 - > 50 mm.

[b]Values include rhizomes.

[c]Percent, by weight, of sample.

[d]Percent, by weight, of total.

Root density decreased at site A below 20 cm. Density at site B remained constant to a depth of 40 cm but decreased markedly below this level. Weights obtained from both sites are consistent with values reported for the root systems of other shrub heathlands (Chapman 1967 and Specht and Rayson 1957).

Distribution of underground organs indicates that fibrous roots (Class 1, 0.1 to 1.0 mm in diameter) were prominent constituents in the root complexes of both heath balds. The percentage of fibrous roots in the first 40 cm of soil was 30% in site A and 42% in B. Fibrous roots decreased below this depth at both sites. Lateral roots, which constitute the majority of Class 2 and 3 roots, had a distribution similar to the fibrous roots. Rhizomes and vertical roots occurred predominantly in Classes 4 and 5 on site A and in Classes 3 and 4 on site B. These underground organs were represented at all depths, with rhizomes near the surface and large roots increasing in importance with depth.

Chemical analyses indicated the presence of caffeic acid, ferulic acid, gallic acid, gentisic acid, hydroquinone, p-hydroxybenzoic acid, 2-pinene, and rhododendrol in size classes of roots.

The root systems of both heath balds contain compounds capable of inducing or contributing to allelopathic interference in soil. These compounds were detected in all size

classes of roots (not including rhizomes), thus affording a potential source of inhibition at every depth. The relationship between phytotoxin concentrations and root size was not examined. Without concentration estimates, the relative importance of the roots at each depth cannot be evaluated. However, as stated earlier, the greatest root density at both sites was recorded in the first 20 cm of soil. The 0-20 cm zone had almost all size classes, and assuming that phytotoxin concentrations and release mechanisms are constant with depth, the first soil zone should be the most toxic to germinating seeds.

II. SOIL

Soil forming processes have the potential to enhance allelopathy in plant communities. Soil physicochemical and biochemical processes provide an opportunity to contribute to the phytotoxic defense against invasion. Phytotoxins introduced from canopy, litter, roots, and microbial degradation of plant residues may be adsorbed on soil colloids. Retention on colloids can increase phytotoxicity by concentrating compounds in strategic soil zones and perpetuating their influence through the year. Conversely, adsorption could also deactivate phytotoxins. Compounds not strongly adsorbed on colloids migrate through the soil, extending influence into other regions.

Regardless of origin, depth, or mobility, phytotoxins

are subject to microbial degradation. At or near the soil surface, compounds may encounter the same synthesis and decomposition processes that occur in litter. Compounds that migrate through soil may be subject to other chemical processes. Different species of soil organisms occupy different positions along chemical gradients in the soil environment. These species have become biochemically adapted to utilize plant residues, phytotoxins, and other food sources (Whittaker and Feeney 1971). Residual presence of phytotoxins in the soil environment represents a balance between microbial degradation and introduction and formation of new compounds (Winter 1961).

Recognizing that phytotoxins can be retained in soil, an investigation was undertaken to assess the importance of heath bald soils in contributing to allelopathy. Soils from each heath bald were periodically analyzed for phytotoxins. The frequency of phytotoxins in the soils was examined, and the inhibitory capabilities of the heath bald soils were determined for each month of the year.

Materials and Methods

Three sampling stations were randomly located on both balds. A 1 x 0.25 m area was defined at each station, from which soil samples were removed at two-week intervals. Soil samples were removed in 5 x 15 cm cores. Samples were taken at the beginning of the investigation from the adjacent Abies

and Quercus/Betula forests. All litter was removed from the cores before they were individually packaged and frozen. Cores were air-dried and screened through a 2 mm mesh sieve to remove roots and stone fragments. Samples were combined by station and month and a single 10 g subsample removed for chemical analysis of phytotoxins (Chapter V, pages 21-25). From the remaining monthly soil samples, a 10 g subsample was removed for bioassay (Chapter V, pages 19-21). Twelve monthly soil samples were used to prepare aqueous leachates for each heath bald.

A two-way analysis of variance with replication was used to test differences in radicle growth of Abies fraseri, Betula lenta, and Tsuga canadensis seeds treated with aqueous soil leachates from the two sites. Product-moment correlation coefficients (r) were calculated between litter and soil bioassays from each site. A second set of correlation coefficients was computed with soil data off-set six months to incorporate a time lag between transfer of phytotoxins from litter to soil.

Results and Conclusions

Chemical survey results of soils from site A are presented in Table 13 and in Table 14 for B. The same eight phenolic compounds were detected in the soils of each heath bald. Six of these compounds were previously identified in the litter. Two additional compounds, caffeic and gentisic

TABLE 13

CHEMICAL SURVEY OF MONTHLY SOIL SAMPLES TAKEN FROM A *RHODODENDRON MAXIMUM* HEATH BALD[a]

Sample Date	Identified Compounds[b]							
	Caffeic Acid	Gallic Acid	Gentisic Acid	Hydroquinone	p-Hydroxybenzoic Acid	Phloroglucinol	Rhododendrol	Vanillic Acid
Feb. (1973)	+	-	+	+	-	++	+++	++
Mar.	-	++	-	++	+	+	++	+++
Apr.	-	-	-	++	+	+	+	+
May	+	++	-	++	+++	++	+	+
June	+	-	++	++	++	-	+++	+++
July	-	-	-	+	+++	+	+++	++
Aug.	-	-	+	-	+	++	+	+
Sept.	-	+	-	+	+++	+	+	+
Oct.	-	-	-	-	+	-	+++	+
Nov.	+	+	+	-	-	+	+	+
Dec.	-	-	+	+	+	-	+	+++
Jan. (1974)	-	+	+	-	++	-	++	+

[a]Compounds extracted from soils and identified by methods described in Chapter V, pages 21-25.

[b](-) Compound not detected in any soil samples.
(+) Compound detected in one soil sample.
(++) Compound detected in two soil samples.
(+++) Compound detected in three soil samples.

TABLE 14

CHEMICAL SURVEY OF MONTHLY SOIL SAMPLES TAKEN FROM A *RHODODENDRON CATAWBIENSE* HEATH BALD[a]

Sample Date	Identified Compounds[b]							
	Caffeic Acid	Gallic Acid	Gentisic Acid	Hydroquinone	p-Hydroxybenzoic Acid	Phloroglucinol	Rhododendrol	Vanillic Acid
Feb. (1973)	-	+	-	+	++	++	+++	+
Mar.	-	++	-	+	+	+	+	+
Apr.	-	++	-	+	-	-	++	++
May	-	-	-	-	++	+++	+	+
June	++	+	-	-	-	+++	+++	++
July	+	++	-	+	++	+	+++	+++
Aug.	-	++	-	-	-	++	++	+
Sept.	-	+	-	-	+	+	+	+
Oct.	-	++	-	-	+	++	+++	++
Nov.	+	+	+	-	+	+	+++	+++
Dec.	+	-	+++	-	-	+	++	+++
Jan. (1974)	-	+	-	-	+	++	++	+

[a]Compounds extracted from soils and identified by methods described in Chapter V, pages 21-25.

[b](-) Compound not detected in any soil samples.
(+) Compound detected in one soil sample.
(++) Compound detected in two soil samples.
(+++) Compound detected in three soil samples.

acids, were also identified. The latter compounds represent contributions from Rhododendron roots. Ferulic acid and 2-pinene were detected in Rhododendron roots but were not found in any of the soil samples. The number of times each compound was detected in the three soil samples of each month is presented in Table 13 for site A and in Table 14 for B. Hydroquinone, p-hydroxybenzoic acid, rhododendrol, and vanillic acid were the most frequently detected compounds at site A. Gallic acid, phloroglucinol, rhododendrol, and vanillic acid compose the group of most frequently detected compounds at site B.

Chemical analysis of Abies forest soil revealed the presence of camphene, α-phellandrene, 2-pinene, caffeic acid, and vanillic acid. The Quercus/Betula soil samples contained gallic and p-hydrocinnamic acids. Both forest soils also contained unidentified compounds.

Bioassays of aqueous soil leachates using Abies fraseri are presented in Figure 5 for sites A and B. Soils collected in all months inhibited radicle growth in Abies. Statistical analysis indicated that variability in radicle growth differs significantly ($P > 0.001$) between soils of sites A and B but not between monthly soil samples. Analysis of site A litter and soil bioassays revealed no significant difference between the two treatments, between monthly samples, or other interactions. Analysis of the relationship between site B litter and soil indicated a highly significant difference ($P > 0.001$)

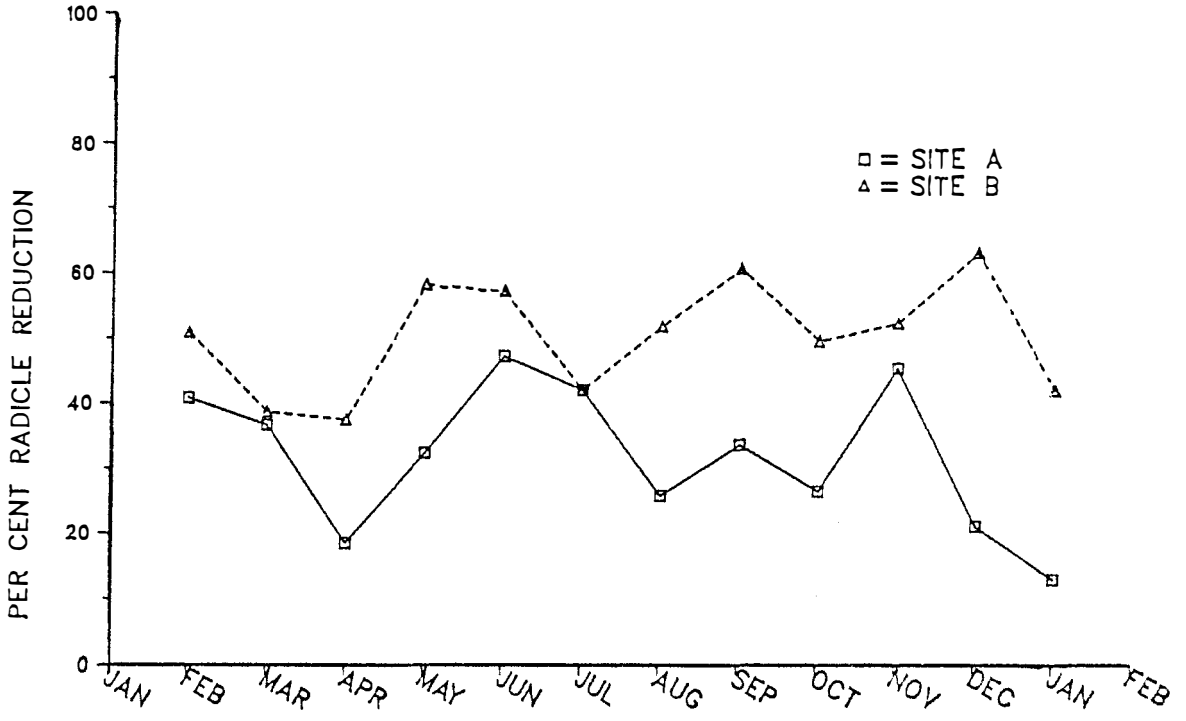

Figure 5. Radicle reduction (percentage of control) of Abies fraseri in monthly soil samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds.

between treatments and no difference between monthly samples or treatment interactions. Lack of significant interaction between treatments is supported by the low r value of 0.18 for site A and 0.48 for B. Calculation of correlation coefficients using a six-month shift in the soil data produced no r values greater than 0.38 for either site. These analyses indicate that the seasonal inhibition pattern produced in Abies fraseri from litter leachates was not repeated in the soil of either heath bald. Lack of a seasonal inhibition pattern may be due to the continual presence of p-hydroxybenzoic acid, rhododendrol, and vanillic acid in the soil of site A and phloroglucinol, rhododendrol, and vanillic acid in the soil of B.

Results of the bioassays using Betula lenta as test material are presented in Figure 6 for sites A and B. Statistical analysis indicated a significant difference ($P > 0.05$) between radicle growth of Betula treated with soil leachates from sites A and B but not between monthly soil samples. Analysis of site A soil and litter bioassays revealed a highly significant difference ($P > 0.001$) between the two treatments but not between their interactions or monthly soil treatments. Results of site B analysis were identical to those of site A. Correlation coefficients between litter and soil were 0.37 for site A and 0.21 for B. These values indicate a lack of association between litter and soil inhibition at both sites. Using the six-month

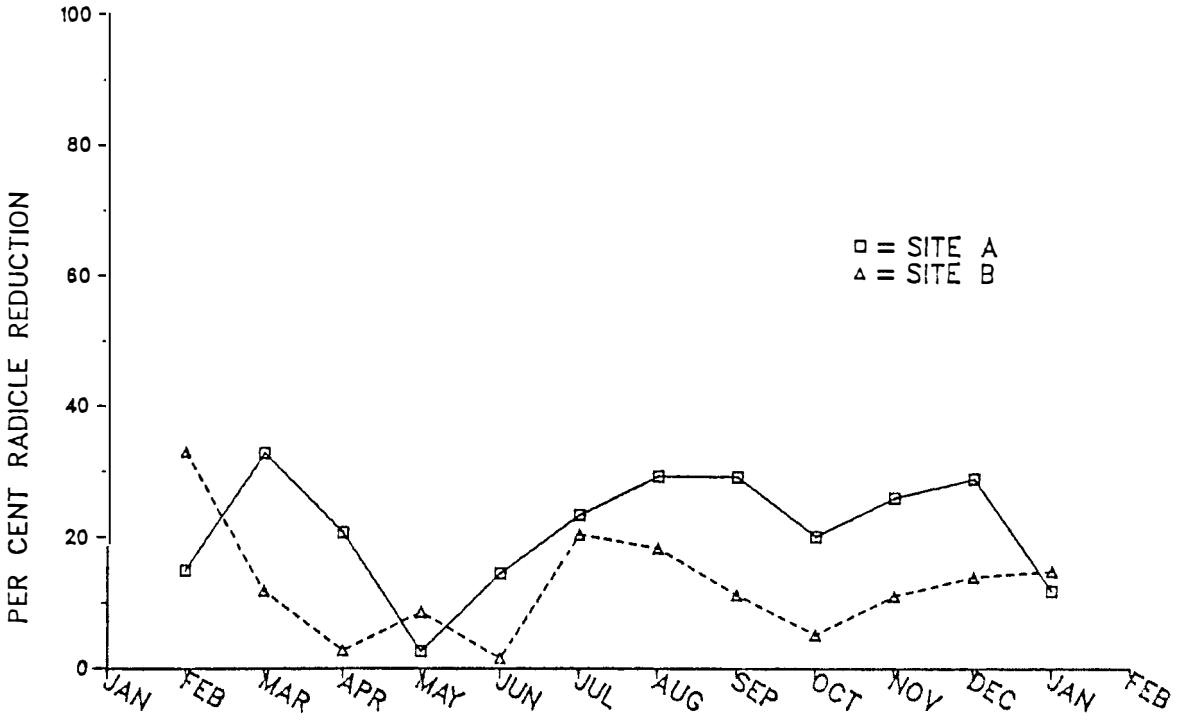

Figure 6. Radicle reduction (percentage of control) of Betula lenta in monthly soil samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds.

shift in soil data, sets of r values were computed for sites A and B. The largest value calculated for site A was 0.51 and 0.55 for B which correspond to four and two month off-sets, respectively. Even these greater values do not indicate a high association between the soil and litter of either site. As with Abies, no seasonal inhibition pattern was found in the soil data of sites A or B. Lack of a seasonal inhibition pattern may be due to the phenolic compounds described for sites A and B by the Abies bioassays.

Bioassay results of Tsuga canadensis treated with sites A and B soil leachates are presented in Figure 7. Soils collected in all months inhibited Tsuga radicle growth. Statistical analysis indicated that radicle growth differed significantly ($P > 0.001$) between the soil treatments of sites A and B. Differences between monthly soil samples were significant ($P > 0.05$) for both sites, but the interactions between litter and soil were not. Analysis of site A litter and soil bioassays indicated differences that were significant between treatments ($P > 0.01$) and between monthly soil samples ($P > 0.05$). Interactions between litter and soil of site A were not significantly different. Analysis of site B revealed highly significant differences ($P > 0.001$) between litter and soil treatments but not between their interactions or the monthly soil samples. The low correlation coefficients of 0.43 for site A and 0.53

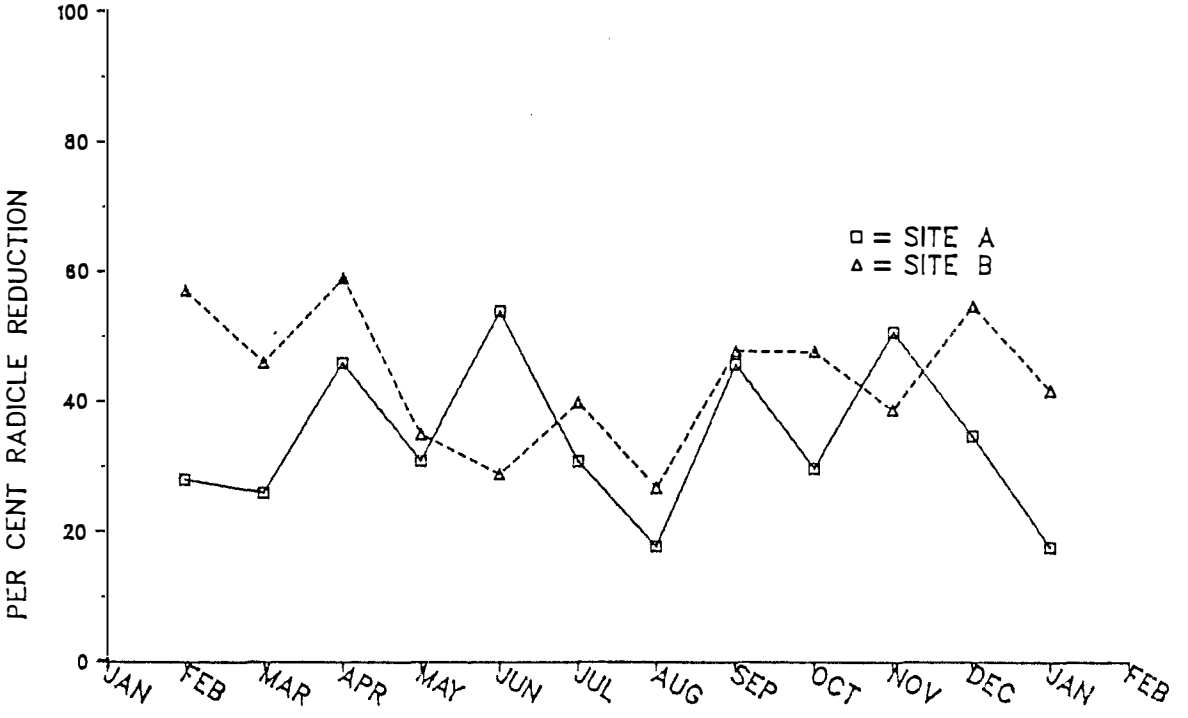

Figure 7. Radicle reduction (percentage of control) of Tsuga canadensis in monthly soil samples from sites A (Rhododendron maximum) and B (Rhododendron catawbiense) heath balds.

for B indicate the lack of significant association between litter and soil. None of the coefficients calculated with time lags were higher than those already presented. Consistent with the other test materials, the inhibition pattern described in the litter of both heath balds was not repeated in the soil. The suite of phenolic compounds defined for Abies may be responsible for the lack of a seasonal inhibition pattern in the soil of sites A and B.

Investigation of the heath bald soil began with a chemical survey of monthly samples from sites A and B. The survey revealed nine phenolic compounds and established their frequency in the soil. Bioassays of site A and B soils were performed for indications of seasonal inhibition. Soil bioassays were subjected to statistical analysis to indicate differences between the soils of each site and between sampling periods. Statistical analyses were conducted on the soil and litter bioassays of each site to reveal differences between treatments, their interactions, and monthly sampling periods. Calculation of correlation coefficients between litter and soil bioassays produced r values that indicated a lack of significant association between treatments. Correlations calculated with time lags in the soil bioassay data provided no indication of seasonal inhibition. The result of these studies has been to establish the inhibitory potential of soil from both heath balds. Demonstration of continuous inhibition on radicle growth of test

species suggests that soil can enhance the allelopathic effectiveness of phytotoxins introduced from the canopy and root systems of both heath bald communities.

CHAPTER X

SENSITIVITY OF FIR, BIRCH, AND HEMLOCK SEEDLINGS TO PHYTOTOXINS

Both recognized and candidate phytotoxins have been detected in aqueous leachates and ethanol extracts of heath bald soils, litters, and canopy components. Species posing the greatest invasion threat to heath balds may not be susceptible to the compounds found at the study sites. The definition of toxicity and species' susceptibility to these suspected phytotoxins is now necessary to establish their allelopathic potential in heath bald communities.

It is beyond the scope of this work to attempt definition of all toxic principles, individual toxicities, and synergistic effects that could be involved in the expression of allelopathic interference at these sites. For this reason, emphasis was on confirming the toxicity of suspected phytotoxins and establishing the concentrations necessary to induce inhibition in the test species.

I. MATERIALS AND METHODS

A fiberglass bioassay technique was chosen for the investigation of suspect phytotoxins (Fuller 1977). Pregerminated seed of Abies fraseri, Betula lenta, and Tsuga canadensis served as test material. Five seeds of a single

species were planted in vials containing wound bundles of Pyrex wool. Each vial was irrigated with 20 ml of either distilled water (control) or test solution. Commercially obtained, spectral-grade compounds were used to test phytotoxicity. The commercial compounds were subjected to the same analytical procedures (Chapter V) used to detect and identify heath bald phytotoxins. Compounds investigated were gallic acid, p-hydroxybenzoic acid, phloroglucinol, rhododendrol, and vanillic acid. A test series composed of 1, 5, 10, and 50 mg/100 ml of distilled water was prepared for each compound. Test vials were incubated in the dark at 25° C. Incubation periods were 96 hours for Abies fraseri, 168 hours for Betula lenta, and 344 hours for Tsuga canadensis.

II. RESULTS AND CONCLUSIONS

Growth inhibition was detected in Abies fraseri for the lowest concentrations of the five phytotoxins tested. Bioassays of the five compounds conducted at four different concentrations are presented in Table 15. Phloroglucinol was the most inhibitory compound at the 1 mg level, and inhibition increased slowly with concentration. Inhibition by vanillic acid, p-hydroxybenzoic acid, and rhododendrol increased with concentration and a significant growth reduction was noted at the 50 mg level for all compounds. Abies' response to gallic acid was minimal for all but the highest concentration. This bioassay indicates that

TABLE 15

THE EFFECT OF CONCENTRATION OF FIVE PHYTOTOXINS ON SEEDLING GROWTH IN ABIES FRASERI

Compound	Concentration (mg/100 ml D. H_2O)			
	1	5	10	50
Gallic Acid	85.6 ± 5.6* (88%)	89.3 ± 4.5 (92%)	95.3 ± 4.5 (98%)	18.3 ± 1.1 (20%)
p-Hydroxybenzoic Acid	96.3 ± 4.7 (99%)	87.3 ± 8.7 (90%)	84.6 ± 4.1 (85%)	20.3 ± 4.9 (21%)
Phloroglucinol	78.6 ± 8.0 (81%)	66.6 ± 0.6 (68%)	53.6 ± 1.1 (55%)	45.6 ± 1.7 (47%)
Rhododendrol	87.3 ± 11.6 (90%)	67.3 ± 8.2 (69%)	68.6 ± 2.1 (70%)	32.3 ± 0.6 (33%)
Vanillic Acid	84.3 ± 9.2 (87%)	80.0 ± 9.8 (82%)	72.3 ± 9.8 (74%)	13.6 ± 4.0 (14%)

*Values are means ± one standard deviation, expressed in millimeters, and the percent radicle growth of the control for three replicates of five seeds each.

germinating seeds of Abies fraseri are susceptible to certain concentrations of all five frequently-detected heath bald phenolics.

Treatment of Betula lenta with the same test series produced the results presented in Table 16. Betula was found to be sensitive to all but vanillic acid in the 1 mg concentration range. Inhibition was noted to increase with concentration of p-hydroxybenzoic acid, rhododendrol, and vanillic acid; the reverse occurred with gallic acid. Gallic acid appears to stimulate the radicle elongation of Betula seeds. No significant relationship was noted between inhibition and concentration of phloroglucinol. This bioassay indicated that all phytotoxins can induce inhibition in Betula. The Betula test material proved generally less sensitive to the concentrations of phytotoxins employed in the bioassay than Abies.

Tsuga canadensis was least inhibited by the phytotoxins in the concentrations used (Table 17). Gallic acid, p-hydroxybenzoic acid, rhododendrol, and vanillic acid increased inhibition with concentration. Phloroglucinol inhibited Tsuga the most at the lowest concentration and stimulated growth at the highest concentrations. These bioassay results indicate that radicle growth can be inhibited in Tsuga by select phenolic compounds. Only p-hydroxybenzoic acid, rhododendrol, and vanillic acid continuously inhibited Tsuga at successively higher

TABLE 16

THE EFFECT OF CONCENTRATION OF FIVE PHYTOTOXINS ON SEEDLING GROWTH IN BETULA LENTA

Compound	Concentration (mg/100 ml D. H_2O)			
	1	5	10	50
Gallic Acid	19.6 ± 2.6* (65%)	21.6 ± 4.1 (72%)	23.3 ± 3.3 (78%)	25.3 ± 1.7 (84%)
p-Hydroxybenzoic Acid	24.0 ± 2.2 (80%)	23.3 ± 2.7 (78%)	18.3 ± 1.0 (61%)	6.0 ± 1.8 (20%)
Phloroglucinol	23.3 ± 1.1 (78%)	21.0 ± 2.9 (70%)	19.3 ± 3.2 (64%)	20.6 ± 2.5 (69%)
Rhododendrol	19.3 ± 1.4 (64%)	18.6 ± 1.0 (62%)	17.3 ± 1.0 (58%)	13.3 ± 2.6 (44%)
Vanillic Acid	30.0 ± 3.2 (100%)	28.0 ± 2.2 (93%)	19.6 ± 3.3 (65%)	11.0 ± 4.1 (37%)

*Values are means ± one standard deviation, expressed in millimeters, and the percent radicle growth of the control for three replicates of five seeds each.

TABLE 17

THE EFFECT OF CONCENTRATION OF FIVE PHYTOTOXINS ON SEEDLING GROWTH IN TSUGA CANADENSIS

Compound	Concentration (mg/100 ml D. H_2O)			
	1	5	10	50
Gallic Acid	41.3 ± 4.1* (113%)	37.3 ± 11.3 (102%)	34.6 ± 5.5 (95%)	17.0 ± 5.0 (46%)
p-Hydroxybenzoic Acid	34.3 ± 6.3 (94%)	29.0 ± 4.0 (79%)	19.0 ± 3.5 (44%)	11.0 ± 1.7 (30%)
Phloroglucinol	29.3 ± 9.5 (80%)	30.0 ± 3.6 (82%)	32.3 ± 7.5 (88%)	43.6 ± 4.7 (119%)
Rhododendrol	35.6 ± 5.1 (97%)	32.3 ± 5.1 (88%)	25.6 ± 5.1 (70%)	11.6 ± 2.0 (32%)
Vanillic Acid	34.3 ± 9.0 (94%)	31.3 ± 4.5 (85%)	28.3 ± 1.1 (77%)	15.3 ± 4.9 (42%)

*Values are means ± one standard deviation, expressed in milliliters, and the percent radicle growth of the control for three replicates of five seeds each.

concentrations. The other compounds promoted growth in Tsuga in a portion of their test range.

The purpose of this analysis was to test the phytotoxicity of five phenolic compounds frequently detected in heath bald leachates. The concentration range selected for these compounds is comparable to phytotoxin concentrations reported in other investigations (Gant and Clebsch 1975). Bioassays of these compounds with three test species indicated that p-hydroxybenzoic acid, rhododendrol, and vanillic acid consistently inhibited the test species. Phloroglucinol did not continuously inhibit all species at all test concentrations. Gallic acid both promoted and inhibited radicle elongation of the test species. As a result of this investigation, three phenolic compounds have been definitively established as general phytotoxins with two compounds indicating limited toxicity.

CHAPTER XI

GREENHOUSE INVESTIGATION

Establishing the presence and mobility of phytotoxins in heath balds does not prove allelopathic inhibition in the field. Similarly, correlation of root radicle inhibition with phytotoxin concentrations in controlled studies is not sufficient to demonstrate allelopathy. Proof of allelopathic interference requires the demonstration of continuing phytotoxin influence on the growth and survival of competitors since without effective residual inhibition, surviving seed would increase competitive pressure to disrupt heath bald integrity.

A greenhouse investigation was designed to examine the effectiveness of selected heath bald components in retarding growth of competitor seedlings.

I. MATERIALS AND METHODS

A 3 x 6 factorial experiment employing a two-way analysis of variance with replication was selected to test the response of Abies fraseri, Betula lenta, and Tsuga canadensis seedlings to different watering and substrate treatments (Sokal and Rohlf 1969). The three watering treatments were distilled water (control) or canopy drip from each heath bald. The six substrate treatments were

soil and litter from each heath bald and soils from the adjacent Abies fraseri and Quercus borealis/Betula lenta forests (control). All treatments were performed in triplicate for each test species.

Duncan's New Multiple Range Test (Steel and Torrie 1960) was applied at the 5% level to each test species to measure the difference among substrate treatment means.

Canopy drip was collected at two-week intervals from 1 m^2 catchments installed at each site. Each collection was filtered and stored under refrigeration. Treatments consisted of two 25 ml applications per week.

Soils were obtained by excavating 10 cm thick blocks from study sites and adjacent forest stands. Soil blocks were trimmed and positioned in clay pots to retain proper orientation. Litter was obtained from materials collected in the litterfall investigation. Litter was ground through a 2 mm sieve before loading into clay pots. Soil and litter treatments were saturated with distilled water prior to planting.

Ten seedlings of either Abies fraseri, Betula lenta, or Tsuga canadensis were planted per pot. After four weeks, the number was reduced to five. Treatment periods ran from 206 days for Abies and Tsuga to 132 days for Betula. Upon completion, the entire seedling was harvested, air-dried, and weighed.

II. RESULTS AND CONCLUSIONS

The results of the statistical analyses are presented in analysis of variance tables for each test species (Tables 18, 19, and 20). The analyses indicate that seedling growth of all test species was not significantly affected by the different watering treatments. Variability in seedling growth among substrate treatments was significant ($P < 0.01$) for all test species. Lack of distinction among watering treatments is attributed to low concentrations of phytotoxins. Although phytotoxins were detected in canopy drip, their contribution was not sufficient to produce seedling growth reduction.

The Duncan's test on *Abies* substrate data indicate that, with the exception of Rm (*Rhododendron maximum*) litter and *Abies* soil, all treatment means were significantly different from each other (Table 21). Heath bald soils were the most inhibitory substrates with Rc (*Rhododendron catawbiense*) and Rm soils producing the greatest degree of inhibition, respectively. Rc litter was the third most toxic substrate. Rm litter and *Abies* soil ranked fourth in growth inhibition. The most productive substrate was *Quercus borealis*/*Betula lenta* (Qb/Bl) soil. The greenhouse investigation further revealed that, with time, Rc litter was a more effective inhibitor of seedling growth than Rm litter.

TABLE 18

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *ABIES FRASERI* SUBJECTED TO THREE WATERING AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatments	17	.0043	
A (substrate)	5	.0123	17.11**
B (watering)	2	.0004	.55 ns
AxB (interaction)	10	.0011	1.63 ns
Error	36	.0007	
Total	53		

$F_{.01[5,36]} = 3.59$ $F_{.01[2,36]} = 5.27$ $F_{.01[10,36]} = 2.69$

TABLE 19

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *BETULA LENTA* SUBJECTED TO THREE WATERING AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatments	17	.9551	
A (substrate)	5	2.5024	24.34**
B (watering)	2	.0785	.76 ns
AxB (interaction)	10	.2567	2.49 ns
Error	36	.1028	
Total	53		

$F_{.01[5,36]} = 3.59$ $F_{.01[2,36]} = 5.27$ $F_{.01[10,36]} = 2.69$

TABLE 20

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *TSUGA CANADENSIS* SUBJECTED TO THREE WATERING AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatments	17	.0245	
A (substrate)	5	.0535	4.59**
B (watering)	2	.0142	1.22 ns
AxB (interaction)	10	.0121	1.04 ns
Error	36	.0116	
Total	53		

$F_{.01[5,36]} = 3.59$ $F_{.01[2,36]} = 5.27$ $F_{.01[10,36]} = 2.69$

TABLE 21

ANALYSES OF GREENHOUSE STUDIES ON THE DIFFERENCES AMONG SEVEN SOIL TREATMENT MEANS EMPLOYING THREE TEST SPECIES[a]

Species	Substrate Treatments					
Abies fraseri	Qb/Bl soil	Rm litter	*Abies* soil	Rc litter	Rm soil	Rc litter
	.286	.255	.251	.231	.201	.186
Betula lenta	Qb/Bl soil	*Abies* soil	Rm soil	Rc soil	Rm litter	Rc litter
	1.635	.662	.591	.282	.218	.022
Tsuga canadensis	*Abies* soil	Rm soil	Rm litter	Qb/Bl soil	Rc soil	Rc litter
	.268	.214	.159	.106	.084	.073

[a]Differences among treatment means were measured by Duncan's New Multiple Range Test applied at the 5% level of significance.

Betula lenta data were segregated into four significantly different groups by the Duncan's test (Table 21). Rc litter produced the greatest inhibition. The second most inhibitory group consisted of Rm litter and Rc soil. Although significantly different from each other, control soils from the surrounding Abies fraseri and Quercus borealis/Betula lenta forests constituted the third and fourth groups, respectively. This investigation extends the bioassay results by confirming the continued inhibition of Betula seedlings by the heath bald substrates.

The Duncan's test separated Tsuga canadensis data into four significantly different groups (Table 21). The most inhibitory group was composed of Rc litter, Rc soil, and Qb/Bl soil. The remaining groups consisted of single treatments decreasing in importance as follows: Rm litter > Rm soil > Abies soil. The long-term inhibition displayed by Rc and Rm litters could not have been predicted from bioassay results. Bioassays indicated that the Rc litter supported better growth than all other substrates while Rm soil was generally more inhibitory than Rm litter. Differences between the two data sets may denote differences in experimental technique. Tannins, terpenes, and other compounds with low water solubility may be present in litter but not in aqueous leachates of litter. The inhibitory effectiveness of these partially soluble compounds would be revealed by growth experiments conducted in litter substrates.

This contention is reinforced by Tsuga growth on Qb/Bl soil. The genus Quercus is a recognized source of tannins and tannin derivatives (Howes 1953). Tannins have recently been identified as inhibitors in climax vegetation (Rice and Pancholy 1973). The presence of tannins and tannin derivates in Qb/Bl soil and rhododendron litters might be the cause of the general lack of growth by Tsuga seedlings.

The greenhouse investigation extended the original conclusions proposed by the litter and soil bioassays. While bicassays indicated the presence and seasonal fluctuations of phytotoxins in heath bald substrates, the greenhouse investigation examined the effects of continual residence on seedling growth. In general, results of the greenhouse investigation support conclusions from the bioassay studies.

CHAPTER XII

FIELD INVESTIGATION

The preceding laboratory and greenhouse investigations were designed to examine phytotoxicity of individual heath bald components while minimizing environmental stress. In the heath bald, environmental stress may increase the effectiveness of phytotoxins. Phytotoxicity can be enhanced or retarded or may remain unchanged by such factors as moisture, temperature, and nutrient availability (Muller 1969). Effectiveness is increased by drought, temperature extremes, and nutrient deficiencies while ample and frequent moisture, adequate nutrients, and uniform temperatures reduce phytotoxicity.

A field investigation was conducted to determine the combined effects of environmental forces and select heath bald components on the growth of competitor seedlings. Information from this investigation could be employed in conjunction with preceding studies for further definition and interpretation of allelopathic interference at the study sites.

I. MATERIALS AND METHODS

A 2 x 4 x 6 factorial experiment was designed to test the response of seedlings of Abies fraseri, Betula lenta,

and Tsuga canadensis to canopy, location, and substrate treatments. Canopy treatments consisted of canopy presence and absence. Location effect was tested by growing seedlings in both heath balds and in the adjacent Abies and Quercus/Betula forests (control). The six substrate treatments were soil and litter from each heath bald and soils from the Abies and Quercus/Betula forests (control). Each treatment was replicated three times.

The effect of canopy was investigated in plots constructed beneath and beyond the canopies of the two heath balds and the Abies and Quercus/Betula forests. Canopy openings equivalent to 1.5 times the height of the surrounding vegetations were cut around each plot.

Location effect was examined by constructing a study plot in each of the four cleared areas and beneath the canopies of both balds and the two adjacent forest communities. A total of eight plots were constructed.

Substrate cubes, 10 x 10 x 10 cm, were exchanged among experimental plots. Cubes were either soil from one of the four communities or litter from one of the heath balds. Study plots were composed of 54 individual cubes, each planted with 10 seedlings of a single test species and initially saturated with distilled water. The investigation was conducted for 150 days for all species.

After examination of preliminary results, a two-way analysis of variance was selected to test the effect of

location and substrate treatments on the growth of the test seedlings. Duncan's New Multiple Range Test was applied at the 5% level to each test species to measure the difference among substrate treatment means.

II. RESULTS AND CONCLUSIONS

All study plots with a canopy resulted in total seedling mortality. In the absence of a canopy, soil and litter cubes failed to establish capillary contact with surrounding soils. Without moisture transfer into the cubes, seasonal rainfall proved inadequate to prevent dehydration. Shrinking accompanied water loss, thus exposing the cube sides and accelerating the drying process. Supplemental water proved ineffective in promoting capillary contact or overcoming desiccation.

Results of the statistical analyses are presented in two-way analysis of variance tables for each test species (Tables 22, 23, and 24). The analyses indicate no significant difference among locations. These results support the greenhouse and bioassay findings that canopy drip from either heath bald does not significantly affect seedling growth. Substrate treatments were found to have a significant ($P < 0.01$) effect on seedling growth of all test species.

The Duncan's test produced similar results for both Abies and Betula seedlings (Table 25). The control soils of Abies and Qb/Bl were not significantly different from each

TABLE 22

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *ABIES FRASERI* SUBJECTED TO FOUR LOCATION AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatments	23	.0056	
A (substrate)	5	.0131	4.71**
B (location)	3	.0023	.83 ns
AxB (interaction)	15	.0038	1.37 ns
Error	48	.0028	
Total	71		

$F_{.01[5,48]} = 3.44$ $F_{.01[3,48]} = 4.24$ $F_{.01[15,48]} = 2.45$

TABLE 23

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *BETULA LENTA* SUBJECTED TO FOUR LOCATION AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatment	23	.0898	
A (substrate)	5	.3316	20.72**
B (location)	3	.0419	2.48 ns
AxB (interaction)	15	.0188	.72 ns
Error	48	.0169	
Total	71		

$F_{.01[5,48]} = 3.44$ $F_{.01[3,48]} = 4.24$ $F_{.01[15,48]} = 2.45$

TABLE 24

TWO-WAY ANALYSIS OF VARIANCE WITH REPLICATION FOR *TSUGA CANADENSIS* SUBJECTED TO FOUR LOCATION AND SIX SUBSTRATE TREATMENTS

Source of Variation	df	MS	F_s
Treatments	23	.0886	
A (substrate)	5	.2648	17.89**
B (location)	3	.0573	3.87 ns
AxB (interaction)	15	.0361	2.43 ns
Error	48	.0148	
Total	71		

$F_{.01[5,48]} = 3.44$ $F_{.01[3,48]} = 4.24$ $F_{.01[15,48]} = 2.45$

TABLE 25

ANALYSES OF FIELD STUDIES ON THE DIFFERENCES AMONG SOIL TREATMENT MEANS EMPLOYING THREE TEST SPECIES[a]

Species	Substrate Treatment					
Abies fraseri	Abies soil	Qb/Bl soil	Rm litter	Rm soil	Rc litter	Rc soil
	.169	.136	.033	.031	.017	.015
Betula lenta	Qb/Bl soil	Abies soil	Rc soil	Rm soil	Rc litter	Rm litter
	.042	.028	.003	.001	.001	.001
Tsuga canadensis	Abies soil	Rm litter	Rm soil	Qb/Bl soil	Rc litter	Rc soil
	.036	.012	.009	.008	.002	.001

[a]Differences among treatment means were measured by Duncan's New Multiple Range Test applied at the 5% level of significance.

other but were significantly different from all other substrate treatments. The soil and litter substrates of Rc and Rm were not significantly different. These analyses indicate that the environment of adjacent forest communities is more favorable to the growth of Abies and Betula seedlings than the heath balds. The substrates of each bald were equally effective in prohibiting seedling growth during the test period. The lack of distinction among heath substrate treatments and subsequently between heath balds may be partially attributed to the experimental design and environmental factors. Use of seedlings prevented determination of influences that might adversely affect viability and germination of overwintering seed. Bioassay investigations indicated that growth of germinating Abies and Betula seeds could be inhibited by winter and spring litter and soil leachates of both balds. Seedlings with underdeveloped or impaired root systems may not have the capability to survive during periods of reduced rainfall (July-October). Failure of Abies and Betula seedlings to become established in the heath bald substrates decreases the competitive pressure from these species.

The Duncan's test segregated Tsuga canadensis data into three significantly different groups (Table 25). The greatest inhibition was exhibited by the group containing Rc soil and litter. The second most inhibitory group included Qb/Bl soil and Rm soil and litter. Abies soil was

least inhibitory. This analysis indicates that the Rc heath bald provided the most unfavorable environment for Tsuga seedlings. The greenhouse and bioassay investigations generally agree with this conclusion. The Rm heath bald was less restrictive to seedling growth than the Rc bald, a conclusion that is also reinforced by the previous investigations. Soil from the Quercus borealis/Betula lenta forest was as unfavorable to seedling growth as the Rm heath bald. The inhibitory qualities of this soil have been recognized in the greenhouse investigation.

The field investigation provides the final data in a series of experiments designed to assess the allelopathic potential of heath bald components. Previous works demonstrated the presence, seasonal fluctuations, relative ranking, and long-term inhibition expressed by heath bald litters and soils. Field studies examined the combined effects of heath bald components and environmental forces on seedling growth. Results show that at both heath balds, inhibition was increased. Previously defined significant differences among heath bald substrates were not detectable for seedlings of Abies and Betula grown on the heath balds.

CHAPTER XIII

SEED RAIN

Most investigations of allelopathy fail to establish the presence of invasion pressure. Lack of seed influx from adjacent communities precludes consideration of allelopathy.

The influx of seeds into a community has been assumed to be an environmental constant but one that has rarely been measured (Wagner 1965). With few exceptions, reports of seed rain have been restricted to descriptions of single species. The net result has been a general lack of comprehensive information about the rate and composition of seed influx into plant communities.

Billings and Mark (1957) noted that seed availability can be an important factor in the persistence of southern Appalachian treeless areas. They proposed that if the deciduous forest is destroyed near its upper limits or the spruce-fit forest near its lower limits, reestablishment may be retarded because the new environment exceeds the tolerance ranges of the seedlings of forest dominants. Destruction of a forest near the tolerance limits of its component species whether along an ecotone between two forests or on the upper or lower timberlines can prolong successional vegetation.

The two heath balds in this study occur in the ecotone

near the upper limits of the Quercus borealis/Betula lenta forest and the lower limits of the Abies fraseri/Picea rubens forest. In this ecotonal position, invasion pressure from the surrounding forests could be diminished by availability of viable seed. For this reason, an investigation was undertaken to estimate the composition, rate, and total annual seed influx into sites A and B.

I. MATERIALS AND METHODS

The 12 litterfall bins described in Chapter VII also served as seed rain collectors. Bins were serviced at monthly intervals for one year. Seeds were sorted, identified, and tabulated.

II. RESULTS AND CONCLUSIONS

Annual seed influx into the sites is presented in Table 26. A limited number of species were collected at each site and of those, only Abies fraseri, Betula lenta, Picea rubens, and assorted unidentified specimens were not ericaceous. The absence of herbaceous seed and the lack of species diversity in the collection reflects the age and composition of the surrounding forests. No attempt was made to incorporate selective sampling techniques of the type described by Wagner (1965) or Gant and Clebsch (1975) for small aerially-borne seed.

TABLE 26

ANNUAL SEED RAIN ON TWO HEATH BALDS

Location	Species	Seeds Per Hectare (10^5)	Percent of Total
Site A	*Abies fraseri*	0.51	2.8
	Betula lenta	4.06	22.6
	Picea rubens	0.71	4.0
	Rhododendron maximum	9.64	53.7
	Vaccinium spp.	2.94	16.4
	Unidentified spp.	0.10	0.5
	Total	17.96	100.0
Site B	*Abies fraseri*	0.91	3.3
	Betula lenta	7.41	27.1
	Picea rubens	1.93	7.1
	Rhododendron catawbiense	7.31	26.8
	Vaccinium spp.	8.93	32.7
	Unidentified spp.	0.81	3.0
	Total	27.30	100.0

Comparison of seed rain values from both sites with those reported for a mature forest community (Wagner 1965) indicated no apparent differences in annual influx. Site A had an annual influx of 17.9×10^5 seed/ha and site B, 27.3×10^5 seed/ha. In the mature forest community, Wagner (1965) reported 16.9×10^5 seed/ha.

The monthly influx of non-ericaceous seed into both sites is presented in Figure 8. With few exceptions, seed influx was continuous through the test period. Few seeds were collected at either location during the summer months, but counts increased during the fall and winter. A major influx occurred at site B during the month of February, which may be due to shattering of the previous year's Betula lenta cones.

The introduction of seed from the dominant species of the surrounding forests establishes availability of competitor seed on both balds. Although the collections were not tested for viability, the quantity of incoming seed and the presence of Abies, Betula, and Picea in the understory (Table 5, page 28) indicates invasion pressure from the adjacent forests.

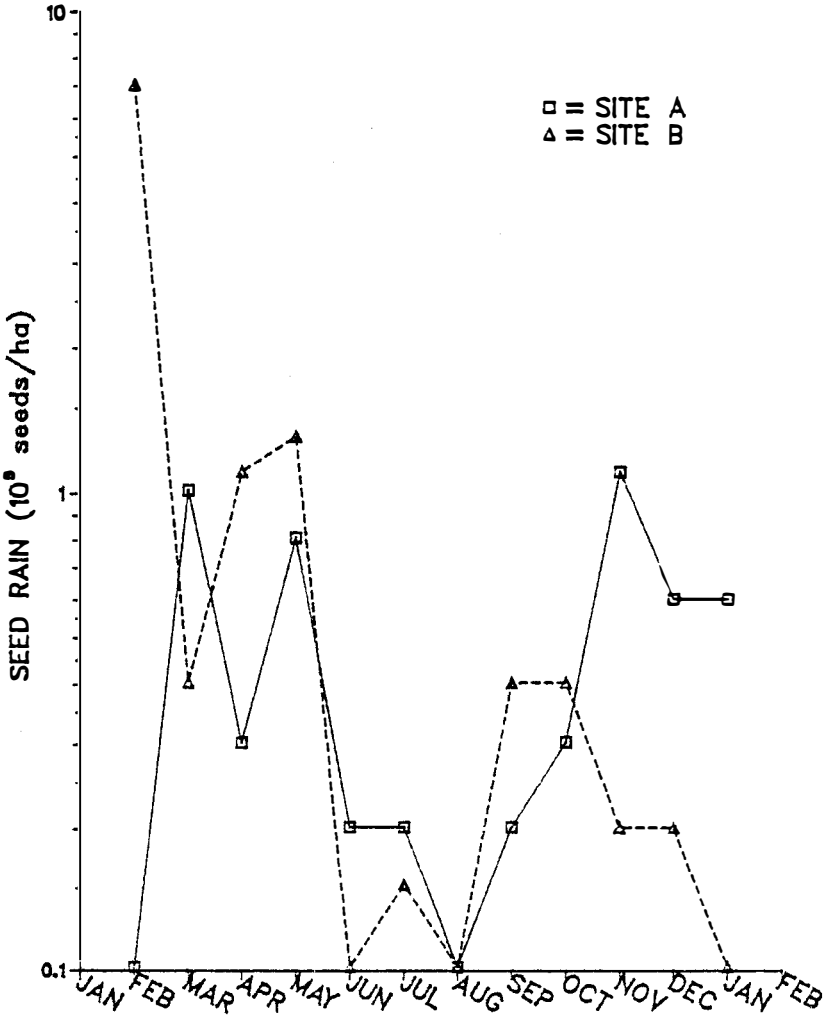

Figure 8. Monthly seed rain on two heath bald communities.

CHAPTER XIV

DISCUSSION

Information has been presented from literature sources and analytical investigations describing southern Appalachian heath balds. Elements of this description will now be examined in the context of ecological theory to determine if they satisfy conditions for persistence. As stated in Chapter II, Holling's (1973) definitions of dynamic stability and resilience will be used to assess persistence of heath balds. Stability is the ability of a system to return to an equilibrium state following a temporary disturbance. The more rapidly and directly the system returns to an equilibrium, the greater is its stability. The region in which the equilibrium occurs is referred to as the domain of attraction. Resilience is defined as the ability of a system to absorb change and disturbance while maintaining the same relationship between populations or state variables, and still persist.

The two heath balds described in this investigation as sites A and B will serve as test cases for persistence.

I. SITE A

The influence of random events on the Rhododendron maximum heath bald may be the key element in the persistence

of this system. Two types of random disturbances have been reported that could influence persistence. Landslide activity has been a major system disturbance on the south-facing slope of site A. All of the vegetation and most of the soil has been lost from the affected areas. Response of the system to this disturbance has been reinvasion of the areas by the heath bald dominants. In the exposed margins surrounding the landslides and on the remaining soil, Rhododendron and Vaccinium are the dominant woody invaders. Rapid reinvasion and establishment of these species will insure recovery of the system to its original state.

The second type of disturbance involves loss of Picea rubens as a canopy competitor. The cause of this disturbance was logging activity, and the system response was closure of the canopy by Rhododendron. This response prevents immediate reestablishment of Picea by requiring invasion beneath the heath bald canopy. Heath phytotoxins, accumulation of litter, and environmental modifications contribute to seedling mortality and decrease the opportunity for reestablishment. This situation is analogous to the shrub heath barrens of Newfoundland (Peterson 1965) that formed following destruction of the forest.

Allelopathic interference is another influence in the maintenance of this heath bald. Phytotoxins present in heath bald litter and soil have been shown to inhibit the germination of the seeds of woody competitors. Environmental

forces interact with phytotoxins to further reduce survival and establishment of competitors in the community. This strategy for persistence has proven effective against all forest associates except Picea rubens. The resistance of Picea to the existing chemical-physical conditions at site A is evident by its presence in the understory. The presence of Picea indicates a deficiency in the allelopathic interference mechanisms of this system. Although allelopathy contributes to maintenance of this system by partially reducing invasion pressure, it is incapable of sustaining the current condition. Reducing invasion pressure prolongs heath dominance and increases the probability of random events controlling the presence of Picea. If Picea is not controlled by other forces, it may eventually disrupt the existing heath bald community.

In Chapter VI, the Rhododendron maximum heath bald was compared to Whittaker's description of a spruce-rhododendron forest heath community. In that discussion, it was proposed that continued success of Picea rubens at site A could result in eventual development of a forest heath. This transition from heath bald to forest heath indicates instability of the system. However, the forest heath should not be interpreted as a separate system competing with the heath bald but as a second equilibrium condition (domain of attraction) in which Rhododendron maximum is a co-dominant with Picea. The tendency for the system to move continually toward the forest

heath indicates that it occupies a lower energy level or a more stable state than the heath bald. Whether the system will achieve the forest heath and establish a stable equilibrium may be determined by random events. The random perturbations caused by landslides, fires, drought, and insect attack would move the system toward the heath bald. By responding to disturbance in this manner, the system can move from one equilibrium condition into another and so persist in a changed configuration.

II. SITE B

The Rhododendron catawbiense heath bald represents a fundamentally different community from that described at site A. While phytotoxins contribute only to the temporary maintenance of A, allelopathic interference plays a decisive role in the persistence of the heath bald on site B. The phytotoxins produced at B interact with climatic forces to prevent successful establishment of woody competitors. The effectiveness of this interaction is evident in Table 5, page 28, where the major competitors, Abies fraseri, Betula lenta, and Picea rubens provide a combined representation of less than 0.7% of the sample. Successful inhibition of competitive species indicates a high degree of system resilience.

The capacity for reinvasion following a physical disturbance is a key requirement for the recovery of any system.

Successful reinvasion of disturbed areas is evident in the margins of landslide areas where Rhododendron and Vaccinium are the primary woody invaders. Lack of intermediate successional stages allows the system to return rapidly and directly to the original equilibrium state. This one-step sequence indicates stability of the heath bald community.

The behavior of this highly resilient system suggests a single distinct domain of attraction, determined by the interaction between allelopathic interference and climatic conditions. When climate supplements allelpathy, the system will inhibit invasion and persist. Long-term climatic changes could disrupt the allelopathic interference mechanism and increase invasion pressure from adjacent forest associates. With only one domain of attraction, the system faces extinction without continual expression of allelopathic interference.

By demonstrating both resilience and stability, the Rhododendron catawbiense heath bald appears capable of sustaining itself and persisting over time until physical disturbance restarts the sequence.

III. SOUTHERN APPALACHIAN HEATH BALDS

The two preceding examples indicate that heath balds are more complex and dynamic than has been previously suggested. For this reason, the present concepts of heath bald existence require modification to properly recognize the

importance of these communities in the vegetation of the southern Appalachian Mountains. A major consideration in any new interpretation must be the recognition that heath balds can occupy more than one stage in the successional sequence of the regional vegetation.

Heath bald species are opportunistic invaders which gain a competitive advantage by efficient seed dispersal and successful seedling establishment in disturbed areas. Rapid seedling growth insures development of a closed heath canopy and the resultant formation of a heath bald. Heath bald species incapable of maintaining dominance by suppressing competitors will be replaced by the adjacent forest community. This type of invasion strategy has been described by Connell and Slayter (1977) in their Tolerance Model of succession. In this concept, successional change begins as a result of disturbance and leads to a community composed of those species most efficient in exploiting resources. Balds developed under these conditions are unstable communities that represent a distinct successional stage which is not the climax vegetation and is not expected to persist.

A modified form of the Tolerance Model (Connell and Slayter 1977) describes the heath community at site A. This type of heath bald follows a secondary successional pattern produced by destruction of the forest canopy. The previously established heath understory closes the canopy and assumes the configuration of a heath bald. By suppressing the

establishment of competitors, allelopathic interference contributes to the maintenance of this community. Because the interference is incomplete, Picea rubens will become established and eventually become the canopy dominant. Unlike the Tolerance Model, the heath species are not eliminated from the later forest community. Shade tolerance and longevity enable the heath species to persist beneath the Picea canopy until disturbance restarts the sequence. Communities of this type will persist and recur in the heath bald domain whenever the system is perturbed.

A third type of heath bald community was described at site B. The Rhododendron catawbiense heath bald is a classic example of Connell and Slayter's (1977) Inhibitory Model of succession. In this model, the primary invaders of disturbed areas gain and maintain control of this space by modifying the environment. The interaction of allelopathic interference and environmental stress prevents the successful establishment of competitive species and effectively arrests succession. The reproductive strategy of the heath species contributes to the continuance of this community type. Production of numerous seed and effective seed dispersal allows rapid colonization of disturbed areas. Rhizome development permits self-replacement of heath shrubs lost by death and disturbance (Horn 1974). Another successful competitive strategy is the longevity of heath species (Drury and Nisbet 1973). The longer life span of the heath shrubs

delays successional change by extending the period of dominance. The Rhododendron catawbiense heath bald represents a community that arrests succession with a combination of competitive factors such as wide dispersal of seed, rapid growth, self-replacement, allelopathic interference, and long life. These factors permit the Rhododendron to be both "early successional" and "climax species" at site B (Drury and Nisbet 1973). Communities of this type represent stable systems that are in equilibrium and can be expected to persist.

These examples of heath bald communities illustrate diversity among community types and their different roles in the succession of regional revetation. Heath balds dominated by Rhododendron catawbiense use allelopathic interference and environmental stress to maintain themselves as distinct shrub communities. These communities represent specific examples in which succession has been successfully arrested. By preventing further succession, these heath balds establish themselves as true climax (sensu Clements 1916) communities. Heath balds dominated by Rhododendron maximum do not resist invasion of forest competitors and therefore cannot maintain themselves. Communities of this type are truly successional.

Allelopathic interference has been identified as a contributing factor in the persistence of some heath bald communities. However, this investigation cannot definitively

establish allelopathy as the controlling factor in these communities. Because chemical analyses were not quantitative, bioassay and field data cannot be completely supported. Acidic soils of the heath balds may reduce availability of nutrients, produce toxic concentrations of metals by dissolving aluminum and iron, and inhibit activity of soil microorganisms (Oosting 1956). These and other factors are recognized as possible controlling influences in the maintenance and persistence of heath balds. Further investigation will be required to establish the role of these factors in heath bald communities.

The broad ecological amplitude of heath balds suggests that they may fill still other roles in the diverse vegetation of the southern Appalachian Mountains. Heath balds can no longer be treated as anomalies in the climax forest but must be recognized as a complex assemblage of shrub-dominated communities. The importance of heath balds can only be assessed by further investigation of those forces that allow the communities to exist and persist in combination with the forest.

IV. RECOMMENDATIONS FOR FUTURE RESEARCH

This investigation indicates the complexity of heath bald communities and the general lack of information about their role in the vegetation of the southern Appalachian Mountains. The results and conclusions presented here pose

further questions about the functioning of individual communities and their relationship with the regional vegetation. Major areas that require further investigation are these:

1. Phytotoxin Concentrations--The phytotoxins identified in heath bald litter and soil should be analyzed to determine individual concentrations during different times of the year. Concentration data could then be used to identify the compounds with the best opportunity to produce allelopathic interference.
2. Modeling of Heath Bald Biochemical Dynamics--Information obtained from this investigation combined with quantitative data could be used to develop a computer model of heath bald communities. The model could then serve as a tool for further investigation of these communities, with specific application to management practices.
3. Alternate Interference Mechanisms--Other potential sources of heath bald maintenance such as metal toxicity, nutrient availability, and predation of invading seeds should be investigated.
4. Heath Bald Inventory--A survey should be undertaken to describe the different types of heath balds that occur in the southern Appalachian Mountains. A compilation of the different

community types and their characteristics would indicate the importance of heath balds in the regional vegetation.

Undoubtedly, there are many other investigations that could be conducted on heath balds that do not relate to their role in succession and stability. However, any research conducted on heath balds should consider those properties that allow these communities to maintain themselves and persist.

CHAPTER XV

SUMMARY

1. The heath balds of the southern Appalachian Mountains provide a distinct contrast to the surrounding forests. The existence of these shrub-dominated communities in the eastern deciduous forest biome suggests the presence of an interference mechanism.
2. Allelopathic interference was investigated as a potential factor in the maintenance and persistence of heath balds. Two properties of ecosystem behavior, resilience and stability, were selected to assess the persistence of heath balds. These relative measures of persistence and the role that allelopathy plays in them was examined.
3. Biochemical surveys of the dominant heath genera, Kalmia and Rhododendron, revealed many potentially phytotoxic compounds. Both genera contain representatives from such important chemical groups as phenols and phenolic acids, terpenoids and steroids, and toxic glycosides.
4. Two heath bald communities located in the Balsam Mountains of western North Carolina were selected as test cases for investigation of allelopathy. The two balds were selected because of their proximity and because they represent communities dominated by a single heath species.

5. Floristic and vegetational surveys indicated that the site designated A was dominated by Rhododendron maximum while site B was dominated by Rhododendron catawbiense.
6. Canopy drip was investigated for presence of phytotoxins and for potentially inhibitory effects on germinating seeds of test species. Three phenolics, hydroquinone, p-hydroxybenzoic acid, and rhododendrol were detected. The phytotoxins in canopy drip were not sufficient to significantly affect radicle growth in the three test species.
7. Both heath bald canopies contributed phytotoxins to litter and soil by loss of leaves, flowers, and woody materials. The major contributor to the litter of both heath balds was Rhododendron leaves. The period of greatest litterfall occurred between June and October and corresponded to the early and late summer shedding of Rhododendron leaves.
8. Phytotoxins contributed from the canopy were not retained in the litter but were lost by leaching and microbial degradation. Continual influx of litter from the canopy supported by a surge in the fall established an inhibition pattern. Maximum inhibition occurred in the summer, declined in the fall and winter, before increasing in spring.
9. The dominant species of both heath balds possessed complex and extensive root systems. Rhododendron roots

were found to contain phenolic and terpenoid phytotoxins capable of supporting allelopathic interference in the soil. The first 20 cm of soil were expected to be the most inhibitory to the germinating and buried seeds of woody competitors.

10. Soil leachates from each heath bald inhibited radicle growth of all test species. Statistical analyses indicated significant differences between the soils of each bald but not between sampling periods. No seasonal inhibition pattern was detected in the soils of either heath bald.
11. Statistical analyses of soil and litter data revealed significant differences between the treatments but not between their interactions. Adjusting data for possible time-lag effect produced no significant correlations between the soil and litter treatments of either bald.
12. Demonstration of continuous inhibition by soil leachates on radicle growth of test species suggests the existence of a successful allelopathic interference mechanism in the soil of both heath bald communities.
13. Bioassay sensitivity analyses were conducted on five phenolic compounds frequently detected in heath bald leachates. Three compounds, p-hydroxybenzoic acid, rhododendrol, and vanillic acid consistently inhibited the test species while gallic acid and phloroglucinol demonstrated limited toxicity.

14. The long-term effect of canopy drip and soil treatments on seedling growth was examined in a greenhouse investigation. Canopy drip was not found to be significantly different from the controls while soil treatments were highly significant. Results of the greenhouse work extended the original conclusions proposed in investigations of soil and litter leachates.
15. The ineffectiveness of canopy drip as a potential allelopathic interference mechanism was confirmed in the field investigation. In this study, soil treatments were found to have a significant effect on the growth of all test species. The combination of soil and environmental stress increased inhibition of seedling growth at both heath balds.
16. Investigation of annual seed rain affirmed the presence of continual invasion pressure from the incoming seed of the surrounding forests.
17. Behavior of the Rhododendron maximum heath community suggests a complex system, possessed of at least two distinct domains of attraction. The current heath bald configuration reflects the system's response to previous disturbances. The spruce-rhododendron forest heath community represents the second and most stable domain of attraction. The system will continually migrate towards the forest heath domain unless disturbance forces it into the heath bald domain. In this manner,

the system can respond to disturbance and persist in a changed configuration.

18. Allelopathic interference delays successional replacement of the Rhododendron maximum heath bald by partially suppressing the establishment and growth of forest competitors. Heath balds dominated by Rhododendron maximum cannot maintain themselves and represent truly successional communities.

19. The Rhododendron catawbiense heath bald is a system with a single domain of attraction, determined by the interaction between allelopathic interference and climatic conditions. Allelopathy contributes to system resilience and is a major force in maintaining the equilibrium stability of this community. The Rhododendron catawbiense heath balds represent stable communities that arrest succession, maintain themselves, and can be expected to persist in the southern Appalachian forests.

20. The results of this investigation pose questions about the current interpretations of heath balds in the southern Appalachian Mountains. Demonstrated diversity among heath balds and their different roles in the vegetation of the region require further definition of these communities. Heath balds must be recognized as a complex assemblage of shrub-dominated heath communities. The importance of the heath balds can only be assessed

by further investigation of those forces that allow these communities to exist and persist in combination with the climax forests of this region.

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VITA

Robert Edward Gant was born November 16, 1946, in Clarksville, Montgomery County, Tennessee. His elementary education was in the Clarksville public school system where he graduated from Clarksville High School in 1964. He matriculated in Austin Peay State University in September 1964 and received a Bachelor of Arts degree from that institution in June 1968.

He entered The Graduate School of The University of Tennessee in September 1968 and received a Master of Science degree from that institution in December 1971. He subsequently applied in June 1972 for admission to doctoral candidacy in The Graduate School of The University of Tennessee, Knoxville. During his training he received an assistantship from The Graduate Program in Ecology to facilitate his research. He holds membership in the Association of Southeastern Biologists, National Association of Environmental Professionals, and Sigma Xi. While attending The University of Tennessee, Knoxville, he has served as an energy and environmental consultant to the Reactor and Energy Divisions of the Oak Ridge National Laboratory from 1972 through 1978.